NOTE TO USERS

This reproduction is the best copy available.

UMI®

University of Alberta

The effect of container type and ectomycorrhizal fungal inoculation on *Pinus contorta* var. *latifolia* plantation establishment: degraded forest soils and planting methods.

By

Donald Bruce Campbell

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta

Spring 2004

Library and Archives Canada

Published Heritage Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et Archives Canada

Direction du Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-96456-6
Our file Notre référence
ISBN: 0-612-96456-6

The author has granted a non-exclusive license allowing the Library and Archives Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Abstract

I conducted two independent field experiments to determine the ectomycorrhizal status and growth of *Pinus contorta* var. *latifolia* seedlings in response to several production and planting variables. Seedlings were grown in Styroblocks™, Copperblocks™, or AirBlocks™, and inoculated with *Rhizopogon rubescens*, *Hebeloma longicaudum*, or left as non-inoculated controls. In one experiment seedlings were planted into manually screefed planting spots or directly into the forest floor, while in the other, seedlings were planted into rehabilitated landings, tilled landings, and unprepared portions of the adjacent cutblock. After two seasons of growth, seedlings planted into manually screefed planting spots exhibited 7% greater growth rates. Forest floor planted seedlings produced 11% more emergent roots with greater ectomycorrhizal colonization. Seedlings planted on fully rehabilitated landings were 60% larger, more vigorous, and exhibited greater growth rates than seedlings planted in the adjacent cutblock. Amongst the manipulated variables, planting environment had the foremost effect on seedling field growth.

Acknowledgements

Forest Renewal British Colombia, and the government of British Columbia through the Forest Innovation Investment Program, provided financial support for this research. Additional financial support and contributions in kind, were generously supplied by Pacific Regeneration Technologies Inc., Canadian Forest Products Ltd., Tolko Industries Ltd., and the British Columbia Ministry of Forests Research Branch.

I would like to thank my supervisors, Dr. Melanie D. Jones and Dr. Janusz J. Zwiazek, for their assistance, guidance, and support throughout the entire process. Additionally I would like to thank Dr. Scott X. Chang, Dr. Philip G. Comeau, and Dr. John Hoddinott for providing valuable comments with regard to the final preparation of this thesis.

A research project of this scope would not have been possible without the support of many companies and individuals. I would therefore like to acknowledge and thank the following: Dr. Chuck E. Bulmer, B.C. Ministry of Forests, Research Branch; Kim Young, Tolko Industries Ltd., Lavington Planer Division; Teresa Raabis, Canadian Forest Products Ltd., Fort St. John / Taylor Operations; Mike Thelitz and Steven Kiiskila, PRT Inc., Red Rock Nursery; Peter Richter, PRT Inc., Vernon Nursery; Wayne Smith, Mikro-Tek Inc.; Pak Chow, University of Alberta; Leanne Philip, University of British Columbia; Leigh Holt, Carl Redmond, and Frann Antignano, Okanagan University College.

Finally, I would like to thank my wife Susan Campbell for her continued support and encouragement, and my son Ross Campbell for his assistance in the field and the lab.

Table of Contents

Chapter 1

General Introduction **1**

Seedling Establishment after Outplanting **1**

Nursery Treatments **3**

Landing Rehabilitation **10**

Forest Floor Planting **14**

Objectives of this Thesis **17**

Literature Cited **20**

Chapter 2

Growth of (1+0) *Pinus contorta* var. *latifolia* seedlings produced in different container types and planted on rehabilitated landings, tilled landings, and cutblocks **34**

Introduction **34**

Materials and Methods **36**

Study Site *36*
Nursery treatments *37*
Seedling Planting *38*
Growth in the Field *39*
Mycorrhizal Status *41*
Soil Analyses *43*
Experimental Design and Data Analysis *45*

Results **46**

Initial Seedling Morphology *46*
Growth in the Field *47*
Mycorrhizal Status *49*
Soil Properties *51*

Discussion **53**

Container Type *53*
Ectomycorrhizal Fungal Inoculation *57*

Landing Rehabilitation *60*

Summary **65**

Literature Cited **66**

Chapter 3

Forest floor planting of *Pinus contorta* var. *latifolia* seedlings in a high-elevation (ESSF) site in north-central British Columbia **92**

Introduction **92**

Materials and Methods **94**

Study Site *94*
Nursery Treatments *95*
Seedling Planting *96*
Growth in the Field *98*
Mycorrhizal Status *100*
Experimental Design and Data Analysis *102*

Results **103**

Initial Seedling Morphology *103*
Growth in the Field *104*
Root Emergence *105*
Mycorrhizal Status *106*

Discussion **108**

Planting Methods *108*
Container Type *110*
Ectomycorrhizal Fungal Inoculation *111*

Summary **116**

Literature Cited **117**

Chapter 4

General Discussion and Conclusions **132**

Container Type **132**

Ectomycorrhizal Fungal Inoculation **134**

Landing Rehabilitation **136**

Forest Floor Planting **137**

Management Implications **139**

Container Type *139*
Fungal Inoculation *140*
Landing Rehabilitation *140*
Forest Floor Planting *141*

Future Research **141**

Literature Cited **143**

Appendix I **148**

Will Lake: Seedling initial stock quality assessment *149*
Will Lake: Seedling Assessment at Lifting *150*
Will Lake: % Colonization at Lifting *153*
Will Lake: Seeding Field Performance *154*
Will Lake: Seedling Harvest *157*
Will Lake: Soils Analysis *160*
Will Lake: Morphotype *164*
Will Lake: Morphotype Relative Abundance *166*

Appendix II **172**

Graham River: Seedling morphology at lifting *173*
Graham River: Root Emergence at Lifting *174*
Graham River: % Colonization at Lifting *176*
Graham River: Soil Mineral Suite *177*
Graham River: Field Performance *17878*
Graham River: Harvest *1811*
Graham River: Seedling Growth Rates *18484*
Graham River: Morphotype *18585*
Graham River: Relative Abundance *18787*

Appendix III **1911**

Ectomycorrhizal Morphological Types *191*

List of Tables

Table 2-1: Morphology of seedlings outplanted at Will Lake..... 78

Table 2-2: Root emergence patterns of seedlings outplanted at Will Lake. 79

Table 2-3: Rooting zone soil physical properties for rehabilitated landings and adjacent cutblock plots at Will Lake. 80

Table 2-4: Rooting zone soil chemical properties for rehabilitated landings and adjacent cutblock plots at Will Lake. 81

Table 3-1: Chemical properties of forest soils in the Graham River study area..... 125

Table 3-2: Morphology of seedlings outplanted at the Graham River. 126

Table 3-3: Root emergence patterns of seedlings outplanted at the Graham River. 127

List of Figures

Figure 2-1: Will Lake field trial study site location. 82

Figure 2-2: Growth rates of seedlings outplanted at Will Lake into tilled landings, rehabilitated landings, or the adjacent cutblock. 83

Figure 2-3: Growth rates of seedlings grown in AirBlocks™, Copperblocks™, or Styroblocks..... 84

Figure 2-4: Relative abundance of the most common ectomycorrhizal morphotypes and overall percent colonization of root tips for seedlings planted at Will Lake. 85

Figure 2-5: Ectomycorrhizal richness, diversity, and evenness, of seedling root tips after two seasons of growth in the field at Will Lake (rooting environment) 86

Figure 2-6: Ectomycorrhizal richness, diversity, and evenness, of seedling root tips after two seasons of growth in the field at Will Lake (container type).. 87

Figure 2-7: Ectomycorrhizal richness, diversity, and evenness, of seedling root tips after two seasons of growth in the field at Will Lake (fungal inoculum)..... 88

Figure 2-8: Relationship between the variation in soil bulk density and carbon concentration at Will Lake..... 89

Figure 2-9: Soil resistance and water content during May and June 2002 at Will Lake..... 90

Figure 2-10: Minimum daily soil temperature at the bottom of the root plug for landings and the adjacent cutblock at Will Lake..... 91

Figure 3-1: Graham River field trial study site location. 128

Figure 3-2: Growth rates of seedlings outplanted at the Graham River following two seasons of growth. 129

Figure 3-3: Relative abundance of the most common ectomycorrhizal morphotypes and overall percent colonization of root tips for seedlings planted at the Graham River. 130

Chapter 1

General Introduction

Seedling Establishment after Outplanting

Reduced initial growth and high mortality of conifer seedlings after outplanting may be the result of both biotic and abiotic factors (McKay 1997) including competition from herbaceous vegetation (Simard *et al.* 2003), poor planting microsite environmental conditions (Krasowski & Owens 2000), and seedling root system architecture (Balisky *et al.* 1995). Naturally regenerated lodgepole pine seedlings develop an initial extensive root system of primary support laterals, which is principally horizontal in orientation and predominantly exploits the upper-most soil horizons (Halter *et al.* 1993; Balisky *et al.* 1995). These horizons encompass the boundary between the mineral soil and the organic layer. Upper soil horizons generally contain more available nutrients (Smethurst 2000) and greater amounts of available water (Phillips *et al.* 2001), and are considerably warmer than lower soil horizons (Sutton 1991). Availability of water and root growth are both affected by soil temperature (Sutton 1991; Wan *et al.* 1999), with mineral soils being consistently below optimal temperatures in central and northern British Columbia (Balisky *et al.* 1995). Initial root growth of newly outplanted styrofoam-block style containerized pine seedlings is primarily restricted to the extension of those lateral roots that have grown down the container walls to the bottom of the root plug. It is the reorientation of the root system, from the natural horizontal orientation to a vertical

orientation, which has become the major concern regarding a majority of container-grown stock (i.e. styrofoam-block style stock). It should be noted, however, that periods of reduced growth and increased mortality are most likely due to poor planting microsite conditions and planting procedures (see below), which are only aggravated by container seedling root architecture (McKay 1997).

Survival and growth of newly outplanted conifer seedlings is dependent upon the roots of the seedlings growing out from the root plug and occupying the surrounding volume of soil (Ritchie & Dunlap 1980; Burdett *et al.* 1983; Halter *et al.* 1993; Scagel & Linderman 2001), thus enabling the seedling to establish a continuum between the substrate and the root plug. Reduced growth and survival of conifer seedlings after outplanting appears to be due primarily to water deficit stress (Grossnickle 1988b; Jiang *et al.* 1995; Eastman & Camm 1995; Girard *et al.* 1997) resulting from an insufficient supply of carbohydrate reserves needed to sustain new root growth (Ritchie & Dunlap 1980; Burdett *et al.* 1983; Girard *et al.* 1997). When planted out, conifer seedlings have only limited carbohydrate reserves, and must begin to actively assimilate carbon in order to grow new tissues. Production of new emergent roots consumes a large amount of fixed carbon and, if reserves are limited, growth is entirely dependent upon newly produced photoassimilate (van den Driessche 1987). If carbon assimilation in the seedling is limited by drought stress, this creates a negative feedback loop where insufficient uptake of water (and associated nutrients) results in reduced assimilation of carbon, which in turn results in root growth that is insufficient to supply the required needs of the seedling (Brissette & Chambers 1992). It is therefore the inhibitory effects of water deficit upon photosynthesis, coupled with insufficient metabolic reserves, which

act to limit growth once seedlings are planted out (Grossnickle 1988a; Grossnickle 1988b). Extended periods of such stagnant growth are commonly referred to as 'planting check' or 'post-planting stress'; they have the potential to greatly increase the time required for stand regeneration and stand rotation (Mullin 1963; Rietveld 1989; Girard *et al.* 1997). Planting check can result in two to three years of stagnant growth for *Pinus contorta* seedlings in the central interior of British Columbia (Burdett *et al.* 1983), while outplanted *Picea glauca* seedlings in northern regions of Ontario may experience ten to fifteen years of lost growth (South & Zwolinski 1997).

Nursery Treatments

Prior to the mid-1970's, forest tree seedlings in British Columbia were outplanted as bare-root stock. The first operationally planted container-grown seedlings were planted near Houston B.C. as a planting productivity trial in 1970 (Vyse *et al.* 1971). Since the mid-1970's, with the establishment of Ministry of Forests test greenhouses around the province, there has been a continual rapid increase in container production of conifer nursery stock (Lavender *et al.* 1998). Vast increases in the number of seedlings required for plantation establishment, higher seedling mortality, increased seed costs combined with lower germination rates, as well as the amount of land required to produce bare-root seedlings, have resulted in a shift towards container-grown stock. Additionally, a fundamental disadvantage of bare-root planting is that contact between the root and soil is broken during lifting. In 1997, Canadian forest-sector companies planted 500,000 hectares with 642,000,000 seedlings (Statistics Canada, 2003). In

British Columbia approximately 220,000,000 seedlings are now planted annually, with bare-root nursery stock accounting for less than 1% of all commercially produced conifer seedlings (Lavender *et al.* 1998; Steven Kiiskila, Personal Communication, 2003). Presently there are three container types used (i.e. Styroblock™, Copperblock™, and AirBlock™) for the commercial production of seedlings in British Columbia, however the question arises as to whether one container type produces a better-quality seedling. The standard Styroblock™ container is the most widely used and is an affordable means of seedling propagation. In Styroblocks™, lateral roots grow until they reach the sides of the block cavities and then grow downwards. This results in the root tips of many of the major lateral roots being located at the bottom of the root plug (Balisky *et al.* 1995). Concern that the resulting root system architecture would lead to toppling in plantation pine stands regenerated from container-grown stock (Mason 1985; Burdett *et al.* 1986) led to modifications of the standard Styroblock™ container. Presently Styroblock™ containers now include vertical ribs to prevent root spiralling. Further modifications to container design have been made in an attempt to modify seedling root systems. One such method is root pruning by either chemicals (e.g., Copperblock™) or air (e.g., AirBlock™) (Burdett *et al.* 1986).

Chemical root pruning is achieved by adding copper formulations such as copper oxychloride (i.e. Copperblock™), copper hydroxide, or cupric carbonate to the interior container walls (Dong & Burdell 1986; Arnold & Young 1991; Dunn *et al.* 1997). Lateral roots contact the container walls and cease growing, thus promoting the generation of new lateral roots (Arnold & Struve 1993), which creates a more dispersed fibrous root system (Lamhamedi *et al.* 2001). Air pruning of lateral roots occurs via a

similar mechanism with lateral roots encountering air due to the many side slits in the cavity wall (Stowe *et al.* 2001; Jones *et al.* 2002b). Air-pruned or chemically pruned root tips are therefore situated along the outer surface of the entire root plug, and can thus presumably access the substrate in any direction (Burdett 1990). This may allow a higher proportion of roots to grow in warmer, more nutrient-rich surface soils (Balisky *et al.* 1995).

Additionally, it should be noted that the perceived concerns regarding one container type, has lead to the design and development of new different container types. The standard Styroblock™ container is the most widely used, primarily due to the fact that it provides an affordable means of seedling propagation. However, concerns regarding potential future stand stability, with respect to the tendency of Styroblocks™ to promote emergent root growth from the bottom of the root plug (Mason 1985; Burdett *et al.* 1986), lead to alterations in Styroblock™ design to facilitate seedling root system modifications. Copper-containing latex solutions were added to the Styroblock™ interior cavity walls, effecting chemical root pruning, thus creating the Copperblock™ container. In addition to the added expense over Styroblocks™, the inclusion of copper formulations has lead to additional concerns regarding leaching of copper as a result of irrigation, as well as block disposal issues. Moreover, Copperblocks™ have a shorter useable block life due to the decrease in copper concentration with each subsequent crop produced, while Styroblocks™ may be used as long as structural integrity is maintained. The AirBlock™ container was subsequently designed to eliminate the problems associated with the Copperblock™, while still effecting root system modification. AirBlocks™, however, require more irrigation because they are made of hard plastic

with many side-slits, which leads to the potting substrate becoming hotter and drier than in Styrofoam containers. On a commercial scale, this necessitates the segregation of AirBlock™ stock to ensure an adequate amount of water is delivered while avoiding over watering of neighbouring Styroblock™ or Copperblock™ stock. Although the AirBlock™ is the more expensive container, higher initial per unit block costs should be alleviated by a significantly longer block life.

It cannot be disputed that copper (Burdett & Martin 1982; Dumroese & Wenny 1997; Aldrete *et al.* 2002) or air (Gingras & Richard 1999; Lamhamedi *et al.* 2001; Gingras *et al.* 2002) root pruning influences the initial root form of planted container seedlings. However the important question is whether this matters with respect to successful plantation establishment and growth towards stand maturity. In a recent study Jones *et al.*(2002b) reported that container type influenced initial root development and seedling growth of lodgepole pine in the nursery, and after the first season of growth subsequent to outplanting. After two years of growth in the field, the authors report that Copperblock™ and AirBlock™ seedlings produced new emergent roots more evenly from all sections of the root plug, while Styroblock™ seedlings produced significantly more new roots from the bottom of the root plug (Jones *et al.* 2002b). In this study, differences in root growth patterns did not result in corresponding variations in the above-ground growth of seedlings. In another recent study, Gingras *et al.* (2002) compared field growth of *Picea mariana* and *P. glauca* produced in air-slit containers. After five years of field growth on different sites, the authors report similar growth, survival, and root system development between seedlings produced in air-slit containers and conventional hard-wall containers. Although some recent studies have investigated

nursery cultural practices with respect to the production of root air-pruned spruce stock (e.g. Lamhamedi *et al.* 2001; Stowe *et al.* 2001), there is a lack of field growth results needed to evaluate air root pruning with respect to future stand establishment of pine. Moreover, spruce seedlings are able to form adventitious roots after planting which often become the primary support lateral roots, while pine seedlings, which have been air or copper root pruned, are dependent upon lateral root growth emerging from those roots that have been pruned due to contact with the container walls (Balisky *et al.* 1995).

Changes in nursery production methods, specifically cultural methods and growing media, have also affected the quality of container-grown seedlings (Steven Kiiskila, Personal Communication, 2003). Bulk density of growing media has decreased significantly, allowing vigorous root growth in the absence of root plug compaction. Additionally, production methods today are such that seedlings are sown at the optimal date to produce the required root and shoot growth, avoiding problems such as root-bound plugs due to excessive time in containers.

Another factor that can affect seedling physiology and root system architecture in the nursery, and hence potentially seedling growth and survival after outplanting, is colonization of roots by ectomycorrhizal fungi (Rajasekaran & Blake 1998; Ditengou *et al.* 2000; Niemi *et al.* 2002). Considerable increases in seedling growth (Marx *et al.* 1988; Walker & Kane 1997; Walker 1999), net photosynthesis (Ekwebelam & Reid 1983; Dosskey *et al.* 1991; Mason *et al.* 2000), stomatal conductance (Runion *et al.* 1997), drought stress tolerance (Dosskey *et al.* 1991; Wu *et al.* 1999; Mason *et al.* 2000), water uptake (Dixon *et al.* 1983; Boyle & Hellenbrand 1991; Mason *et al.* 2000), and root hydraulic conductance (Cui & Nobel 1992; Muhsin & Zwiazek 2002a; Muhsin &

Zwiazek 2002b) have been widely reported for ectomycorrhizal seedlings. Inoculation with specific ectomycorrhizal fungi in the nursery can endow seedlings with significant increases in growth prior to lifting (e.g. Parladé *et al.* 2001) over those from typical nursery fungi, while inoculation with other ectomycorrhizal fungi can cause growth depression (Amitava *et al.* 2002; Jones *et al.* 2003). Growth depression may result because ectomycorrhizal fungi obtain their carbon as photosynthate from the host plant (Smith & Read 1997), and therefore ectomycorrhizal root systems generate a greater demand for photosynthate than do non-mycorrhizal roots (Ekwebelam & Reid 1983).

Ectomycorrhizae may increase drought resistance of seedlings, which is thought to result from protecting roots from shrinkage and providing an increase in water uptake from soil at low water potentials by the fungal hyphae (Augé & Duan 1991; Duan *et al.* 1996; 2000). Evidence in support of this hypothesis (Boyle & Hellenbrand 1991) reveals an increase in drought tolerance due to the ability of ectomycorrhizal roots to take up water against a steeper gradient than non-mycorrhizal roots. While ectomycorrhizae could not provide the means to overcome extended periods of severe drought, the protective effects of the fungi enabled colonized roots to recover more rapidly and at lower soil water potential from drought cycles (Mukerji *et al.* 2000). Additionally, seedling root tip growth and root system architecture are modified by the ectomycorrhizal relationship (Smith & Read 1997); however, the resultant ectomycorrhizal root morphology is dependent upon the host species and the fungal partner (Martin *et al.* 2001). Although a majority of these studies have been completed under laboratory conditions, results provide evidence to support the hypothesis that

ectomycorrhizal fungal inoculation can potentially enhance seedling growth and performance both in the nursery and after outplanting.

Field trials have demonstrated that growth response to seedling inoculation is dependent upon both the fungus and the planting site (Browning & Whitney 1992); however, growth stimulation can be long-lasting, especially on harsh sites, under drought conditions, or with plantation tree species that are not native to an area (LoBuglio & Wilcox 1988; Marx *et al.* 1988; Garbaye & Churin 1997). In other cases, any growth stimulation in the nursery disappears with time. This may be because, if planted on a recently logged site, seedling roots gradually become colonized with ectomycorrhizal fungi native to that site (Hagerman *et al.* 1999; Jones *et al.* 2002a) and thus can supplant the inoculated ectomycorrhizal fungi. Thus, the benefits of nursery inoculation of seedlings destined for recently logged productive sites are still uncertain.

Although the ectomycorrhizal status of containerized nursery stock has been examined (Bledsoe *et al.* 1982; Roth & Berch 1992; Berch & Roth 1993), very little is known about the potential interaction between different container types and ectomycorrhizal fungal inoculation in the nursery. Past research, with respect to container types and inoculation techniques, has focused on the effectiveness of different types of ectomycorrhizal fungal inocula (i.e. spore, mycelial, vegetative) in the establishment of ectomycorrhizas on container-grown root systems (Castellano *et al.* 1985; Boyle *et al.* 1987; Marx *et al.* 1989). Other earlier studies have been conducted to investigate the inoculation potential of a specific ectomycorrhizal fungus with different species of container-grown host seedlings (Marx *et al.* 1982; Valdés 1986; Duñabeitia *et al.* 1996), or a single container-grown host species with different ectomycorrhizal fungi

(Molina 1979; Grossnickle & Reid 1982; Browning & Whitney 1992). Recently still other studies have investigated different nursery cultural regimes, such as fertilization and irrigation, in conjunction with inoculation of containerized seedlings (Walker & Kane 1997; Quoreshi & Timmer 2000; Khasa *et al.* 2001). Although some of these studies have compared containerized seedlings and bare-root stock with respect to colonization by ectomycorrhizal fungi, there is a lack of research regarding container type and ectomycorrhizal fungal inoculation as independent variables. In the only published study that partially addresses this question, Ruehle (1985) investigated the potential effects of exposure to cupric carbonate (i.e. copper root pruning), on containerized inoculated pine seedlings, concluding that $CuCO_3$ exposure, in conjunction with inoculation of *Pisolithus tinctorius*, resulted in the potential for seedlings to produce long lateral roots in the upper portion of the root plug. Ruehle (1985) also found that exposure to $CuCO_3$ had various effects on formation of ectomycorrhizas following inoculation, and was dependent upon the host species. In this study, cupric carbonate increased ectomycorrhiza formation on *Pinus palustris* and decreased formation on *P. strobus*, and had no effect on *P. taeda* and *P. echinata* (Ruehle 1985).

Landing Rehabilitation

Operational ground based forestry operations typically require the construction of access structures such as haul roads, skid trails, and log landings. In British Columbia, Timber Harvesting Practices Regulations (Forest Practices Code of British Columbia Act 1995, amended 2003) require that all temporary access structures (roads, landings, and

trails) be rehabilitated to restore site productivity and returned to productive forest, if they are not required for long-term management of the site. In the interior of British Columbia, temporary access structures occupy approximately 5% of the harvested portion within the operational forest (British Columbia Ministry of Forests 2000). Therefore if these access structures could be successfully returned to productive forest, this would represent a significant increase in the amount of land available for producing marketable timber. Additionally, this increase in the land base of the operational forest, would result in analogous gains in the Long Run Sustainable Yield and Allowable Annual Cut (Bulmer & Curran 1999).

Degraded forest soils resulting from ground-based harvest operations, specifically the building of temporary access structures, are often characterized as supporting only limited growth of plantation conifer seedlings (Arnott *et al.* 1988; Miller *et al.* 1996; Dykstra & Curran 2000). Successful rehabilitation of excavated and bladed skid trails has been reported via re-contouring of the existing slope using side cast material and preservation of the original top soil layer (Dykstra & Curran 2000). Rehabilitation of temporary haul roads by mechanical tilling has produced mixed results (e.g. McNabb 1994; Luce 1997), primarily due to excessive soil compaction from loaded log trucks and heavy equipment, and displacement of surface horizons during construction.

Landings provide a central location where harvesting activities such as decking, processing, loading, and the piling and disposal of slash take place. Construction and subsequent use of landings severely alters the forest soil. Landings are typically constructed by scraping away surface soil horizons, followed by subsoil cutting and

filling to level the site (Plotnikoff *et al.* 2002). Furthermore, soil compaction occurs, both during and after landing construction, due to extensive heavy machine traffic including loaded log trucks (Jansson & Wästerlund 1999). Once harvesting operations are concluded, landings are typified by nutrient-poor, compacted soils (Bulmer 1998).

Soil compaction is characteristically described as the increase in soil bulk density resulting from a rearrangement of soil particles, in response to the application of an applied external force (Roberts 1996). Thus, soil compaction results in an increase in soil bulk density associated with a decrease in soil volume (de Gouvenain 1996). Soil compaction and its associated effects can potentially last for decades (Sutton 1991; Croke *et al.* 2001). Some of these effects include a reduction in the number of large soil macropores and an increase in the number of small pores, resulting in increased (less negative) soil matrix potential (de Gouvenain 1996); higher thermal conductivity (Sutton 1991); increased strength, which in turn restricts root growth through mechanical impedance (Heilman 1981); and altered nutrient availability by reducing the mobility of inorganic ions, water, and air (Williamson & Neilsen 2000; Arocena 2000). Because of these changes in physical properties, compacted soil contains less available water even though it may contain more water overall. Moreover, soil compaction adversely affects site hydrology by increasing soil surface run off and erosion (Croke *et al.* 2001). Bulk density is, therefore, a crucial soil property affecting the portion of the surrounding soil environment that a newly planted seedling must access in order to survive and sustain growth. Seedlings growing on sites with increased soil bulk density, as a result of soil compaction, must have larger root systems in order to obtain the same amount of nutrients and water as seedlings on less compacted soil. Thus, soil compaction tends to

reduce seedling growth and root system development, which in turn can adversely affect root to shoot ratios and shoot nutrient mineral status for many years (Greacen & Sands 1980; Conlin & van den Driessche 1996), resulting in plantation failure or a significant increase in time towards stand rotation.

Removal of the forest floor, through displacement of upper soil horizons during landing construction, also acts to depress seedling growth (Radwan 1992; Prescott *et al.* 2000; Gomez *et al.* 2002) through decreased nutrient levels. Moreover, forest organic soil horizons generally contain the highest concentration of ectomycorrhizae (Fleming *et al.* 1984; Harvey *et al.* 1997; Simard *et al.* 1997); therefore, their removal reduces the level of potential ectomycorrhizal inoculum. Thus the overall effect of landing construction and subsequent usage, is the significant decrease in site plant productivity (Bulmer 1998). Consequently, if landings are to be returned to productive forest, the conditions that resulted in diminished productivity must be alleviated.

Rehabilitation of landings has been attempted via various methods in the past. Alleviation of soil compaction through mechanical tillage or ripping has been employed (McNabb 1994; Luce 1997; Bulmer 2000; Plotnikoff *et al.* 2002), while restoration of nutrients and organic matter has also been attempted via various methods such as the addition of sewage sludge (McNab & Berry 1985), fertilizer (Carr 1987), nutrient-rich plant waste (Bauhus & Meiwes 1994), topsoil (Kranabetter & Osberg 1995), pulp fibre waste (Kranabetter & Bulmer 1995), wood chips and sawdust (Bulmer 2000); or by establishing N-fixing plants (Power 1994). Although some methods have resulted in successful landing rehabilitation (Bulmer 2000), rehabilitation success is related to the

severity of the alteration of the original site characteristics required for the construction of the landing, as well as the soil type (Sutton 1991).

Alleviation of soil compaction alone may be sufficient to restore site productivity, especially on coarse-textured soils (Bulmer 2000), if landings are not deficient in organic matter as a source of nutrients for planted seedlings (Rees & Jackson 2001). Plotnikoff *et al.* (2002), in a retrospective study, investigated 88 landings, from three separate Forest Districts in the interior of British Columbia, which were operationally de-compacted and seeded with a mixture of grass and legumes, and planted with lodgepole pine. They found that compaction alleviation and cover crop seeding generally resulted in successful plantation establishment; however, results varied with respect to soil type, nutrient levels, and the effectiveness of soil de-compaction (Plotnikoff *et al.* 2002). Rehabilitation success is often reduced on landings with fine textured soils (Bulmer & Curran 1999; Sanborn *et al.* 1999; Plotnikoff *et al.* 2002), and although methods to restore organic matter to the landing may initially alleviate low nutrient levels, these methods generally provide short-term benefits only (Carr 1988; Bulmer 1998; Qualls 2000). Of additional concern is the fact that, for the most part, these methods to restore landing nutrients levels are associated with high implementation costs and increased logistics, preventing a majority of these methods from being used widely.

Forest Floor Planting

On many plantation sites in British Columbia, conifer seedlings have customarily been planted in screefed (i.e. scrape away organic horizons and expose mineral soil)

planting spots, which can be created either by manual means or by heavy equipment such as an excavator. Screefing, is an important silvicultural tool for creating a favourable rooting environment for newly outplanted conifer seedlings (Burton *et al.* 2000; Bock & van Rees 2002; Fraser *et al.* 2003). Field trials have demonstrated that screefed planting spots decrease competition from herbaceous species (Cain 1996; Simard *et al.* 2003), increase available nutrients and water (Grossnickle & Heikurinen 1989; Radwan 1992), and increase soil temperature (Delong *et al.* 1997), thus providing a more sheltered planting microsite (Lavender *et al.* 1998; Heineman 1998). However, when screefing is done mechanically, some site characteristics may be adversely affected (Sutherland & Foreman 2000). Schmidt *et al.* (1996) compared forest soil exposed to various mechanical treatments (trenching, ripping, and blade screefing) with the forest floor of areas with no mechanical treatment. They concluded that mechanical site preparation, regardless of the method, tended to reduce the available nitrogen and phosphorus while increasing soil pH and base saturation. The authors attributed the resultant impact on soil chemical properties to the amalgamation and dislocation of soil during treatment, which tended to increase with the level of disturbance and removal of the forest floor (Schmidt *et al.* 1996). Mechanical site preparation tends to compact forest soils, resulting in the changes to soil physical properties described above (Miller *et al.* 1996). Manual or boot screefing (where tree planters scrape or screef away the upper soil horizons to expose the mineral soil) creates planting spots similar to the ones created by mechanical treatment, except that they are smaller in size (i.e. approximately 0.1 m^2 manual and 1.5 m^2 mechanical). The small patches produced by manual spot screefing also reduce the potential of frost heaving of seedlings (Sahlén & Goulet 2002), which can be a problem

in the larger mechanical patches. Manual spot screefing is typically employed on unprepared sites where mechanical site preparation is difficult or impossible (i.e. steep slopes or in partial cut harvest situations).

Planting seedlings directly into the undisturbed forest floor has been recently proposed in order to reduce high machinery costs and soil compaction associated with mechanical site preparation, and because mechanical site preparation may not be possible on adverse terrain (Balisky *et al.* 1995; Heineman 1998). Additionally, more attention is now focused on optimal microsite selection during operational outplanting as tree planters select locations that reduce growth limiting factors, as opposed to regimented planting to simply satisfy stocking density (Lavender *et al.*1998). Forest floor planting also has the potential to decrease planting costs, as seedlings can be planted much faster when compared to manual spot screef planting.

The forest floor has the potential to provide an ideal environment for seedling growth: it has low bulk density, good aeration, available nutrients, ectomycorrhizal fungal inoculum, warmer temperature, and available water (Radwan 1992; Hallsby 1995; Balisky *et al.* 1995). As previously stated, naturally regenerated conifer seedlings develop a horizontally oriented root system exploiting the upper mineral soil horizons, with concentrations of fine roots often observed near the boundary layer of the mineral soil and the organic layer. Availability of water and root growth are both adversely affected by soil temperature (Lopushinsky & Max 1990; Landhäusser *et al.* 2001; Peng & Dang 2003) with mineral soils in northern and the central interior of British Columbia being consistently below optimal temperatures (Balisky *et al.* 1995). Below optimal root zone temperature has been identified as the overriding factor responsible for poor conifer

plantation establishment and success in northern and central British Columbia (Balisky & Burton 1997). Planting seedlings directly into the forest floor such that the upper portion of the root plug is located in the warmer, nutrient-rich, organic horizon, while the bottom of the root plug is located in the mineral soil, may help to alleviate sub-optimal mineral soil temperatures (Balisky *et al.* 1995).

Objectives of this Thesis

The root systems of lodgepole pine seedlings can potentially be affected by both container type and colonization by ectomycorrhizal fungi; however, little is known about the potential interaction between these two factors. Rehabilitation of log landings and temporary roads is required for many forest sites in British Columbia; however, more information is needed regarding practical methods to return landings to productive forest using materials found on site. Increased logging on precipitous terrain, and a decline of mechanical site preparation, has resulted in a change in focus regarding potentially suitable planting substrates. Therefore the overall objectives of this thesis research were:

1) To compare the shoot growth and root growth potential, at lifting, of interior lodgepole pine seedlings produced in Styroblocks™, Copperblocks™, or AirBlocks™, and inoculated with *Rhizopogon rubescens, Hebeloma longicaudum,* or non-inoculated controls;

2) To contrast the growth and development of the same interior lodgepole pine seedlings after two years of growth in the field;

3) To determine whether practical methods, using materials found on site, would restore the productivity of log-landings to that of the adjacent cutblocks;

4) To compare the growth and development of seedlings in manual spot- screefed planting microsites with those planted in the forest floor (raw planted).

This thesis describes the results of two independent studies. The first study (Chapter 2) addressed objectives 1, 2 and 3 for frozen-stored spring-planted lodgepole pine stock. Specifically, this study was designed to assess two different landing rehabilitation methods in comparison with the adjacent cutblock. Therefore seedlings were planted into three different rooting environments. At lifting, seedlings were assessed for stem growth, root emergence, and ectomycorrhizal colonization. Subsequent to outplanting, seedlings were assessed for stem growth after each of the first two growing seasons, and for root emergence and ectomycorrhizal status at the end of the second growing season. Seedling growth, development, and ectomycorrhizal status were subsequently used to determine the effectiveness of landing rehabilitation treatments with respect to the adjacent cutblock.

The second study (Chapter 3) addressed objectives 1,2 and 4 for hot-lifted, summer-planted stock. Lodgepole pine seedlings were either planted into manually spot-screefed planting spots, or were planted directly into the undisturbed forest floor. Seedlings were assessed at the same times as the first study. Seedling growth,

development, and ectomycorrhizal status, were therefore used to compare spot screef planting with forest floor planting.

The final chapter of this thesis (Chapter 4) summarizes the results from the two studies. This chapter includes management implications in order to provide relevant information to assist in decisions regarding lodgepole pine nursery stock, planting methods, and rehabilitation of degraded forest soils. Additionally, suggestions for future research are included.

Literature Cited

Aldrete, A., Mexal, J.G., Phillips, R., and Vallotton, A.D. 2002. Copper coated polybags improve seedling morphology for two nursery-grown Mexican pine species. For. Ecol. Manage. 163: 197-204.

Amitava, R., Bhadoria, P.B.S., Das, D.K., and Rakshit, A. 2002. An overview of mycorrhizal symbioses. J. Interacademicia 6: 570-581.

Arnold, M.A. and Struve, D.K. 1993. Root distribution and mineral uptake of coarse-rooted trees grown in cupric hydroxide-treated containers. HortScience 28: 988-992.

Arnold, M.A. and Young, E. 1991. $CuCO_3$-painted containers and root pruning affect apple and green ash root growth and cytokinin levels. HortScience 26: 242-244.

Arnott, J.T., Carr, W.W., and Waines, A.C. 1988. Establishing forest cover on winter landings in the central interior of British Columbia. For. Chron. 64: 121-126.

Arocena, J.M. 2000. Cations in solution from forest soils subjected to forest floor removal and compaction treatments. For. Ecol. Manage. 133: 71-80.

Augé, R.M. and Duan, X. 1991. Mycorrhizal fungi and nonhydraulic root signals of soil drying. Plant Physiol. 97: 821-824.

Balisky, A.C. and Burton, P.J. 1997. Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in the interior British Columbia. New For. 14: 63-82.

Balisky, A.C., Salonius, P., Walli, C., and Brinkman, D. 1995. Seedling roots and forest floor: misplaced and neglected aspects of British Columbia's reforestation effort? For. Chron. 71: 59-65.

Bauhus, J. and Meiwes, K.J. 1994. Potential use of plant residue wastes in forests of northwestern Germany. For. Ecol. Manage. 66: 87-106.

Berch, S.M. and Roth, A.L. 1993. Ectomycorrhizae and growth of Douglas fir seedlings preinoculated with *Rhizopogon vinicolor* and outplanted on eastern Vancouver Island. Can. J. For. Res. 23: 1711-1715.

Bledsoe, C.S., Tennyson, K., and Lopushinsky, W. 1982. Survival and growth of outplanted Douglas fir seedlings inoculated with mycorrhizal fungi. Can. J. For. Res. 12: 720-723.

Bock, M.D. and van Rees, C.J. 2002. Mechanical site preparation impacts soil properties and vegetation communities in the Northwest Territories. Can. J. For. Res. 32: 1381-1392.

Boyle, C.D. and Hellenbrand, K.E. 1991. Assessment of the effect of mycorrhizal fungi on drought tolerance of conifer seedlings. Can. J. Bot. 69: 1764-1771.

Boyle, C.D., Robertson, W.J., and Salonius, P.O. 1987. Use of mycelial slurries of mycorrhizal fungi as inoculum for commercial tree seedling nurseries. Can. J. For. Res. 17: 1480-1486.

Brissette, J.C. and Chambers, J.L. 1992. Leaf water status and root system water flux of shortleaf pine (*Pinus echinata* Mill.) seedlings in relation to new root growth after transplanting. Tree Physiol. 11: 289-303.

Browning, M.H.R. and Whitney, R.D. 1992. Field performance of black spruce and jack pine inoculated with selected species of ectomycorrhizal fungi. Can. J. For. Res. 22: 1974-1982.

Bulmer, C.E. 1998. Forest soil rehabilitation in British Columbia: a problem analysis. B.C. Ministry of Forests. Land Management Handbook. Victoria, B.C. Rep. LMH-44.

Bulmer, C.E. 2000. Reclamation of forest soils with excavator tillage and organic amendments. For. Ecol. Manage. 133: 157-163.

Bulmer, C.E. and Curran, M. 1999. Retrospective evaluation of log landing rehabilitation on coarser textured soils in southeastern British Columbia. B.C. Ministry of Forests. Extension Note. Victoria, B.C. Rep. EN-042.

Burdett, A.N. 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. Can. J. For. Res. 20: 415-427.

Burdett, A.N., Coates, H., Eremko, R., and Martin, P.A.F. 1986. Toppling in British Columbia's lodgepole pine plantations: significance, cause and prevention. For. Chron. 62: 433-439.

Burdett, A.N. and Martin, P.A.F. 1982. Chemical root pruning of coniferous seedlings. HortScience 17: 622-624.

Burdett, A.N., Simpson, D.G., and Thompson, C.F. 1983. Root development and plantation establishment success. Plant Soil 71: 103-110.

Burton, P., Bedford, L., Goldstein, M., and Osberg, M. 2000. Effects of disk trench orientation and planting spot position on the ten-year performance of lodgepole pine. New For. 20: 23-44.

Cain, M.D. 1996. Woody and herbaceous competition effects on the growth of naturally regenerated loblolly pine and shortleaf pines through 11 years. New For. 14: 107-125.

Carr, W.W. 1987. Restoring productivity on degraded forest soils: Two case studies. Government of Canada, Province of British Columbia. Forest Resource Development Agreement. Victoria, B.C. Rep. FRDA 002.

Carr, W.W. 1988. Nutritional and soil compaction aspects of establishing forest cover on winter landings in the Fort St. James area. Can. For. Serv. and B.C. Min. For. Victoria, B.C. Rep. FRR 047.

Castellano, M.A., Trappe, J.M., and Molina, R. 1985. Inoculation of container-grown Douglas fir. seedlings with basidiospores of *Rhizopogon vinicolor* and *R. colossus*: effects of fertility and spore application rate. Can. J. For. Res. 15: 10-13.

Conlin, T.S.S. and van den Driessche, R. 1996. Short-term effects of soil compaction on growth of *Pinus contorta* seedlings. Can. J. For. Res. 26: 727-739.

Croke, J., Hairsine, P., and Fogarty, P. 2001. Soil recovery from track construction and harvesting changes in surface infiltration, erosion and delivery rates with time. For. Ecol. Manage. 143: 3-12.

Cui, M. and Nobel, P.S. 1992. Nutrient status, water uptake and gas exchange for three desert succulents infected with mycorrhizal fungi. New Phytol. 122: 643-649.

de Gouvenain, R.C. 1996. Indirect impacts of soil trampling on tree growth and plant succession in the north cascade mountains of Washington. Biol. Conserv. 75: 279-287.

Delong, H.B., Lieffers, V.J., and Blenis, P.V. 1997. Microsite effects on first-year establishment and over winter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. 27: 1452-1457.

Ditengou, F.A., Béguiristain, T., and Lapeyrie, F. 2000. Root hair elongation is inhibited by hypaphorine, the indole alkaloid from the ectomycorrhizal fungus *Pisolithus tinctorius*, and restored by indole-3-acetic acid. Planta 211: 722-728.

Dixon, R.K., Pallardy, S.G., Garrett, H.E., Cox, G.S., and Sander, I.L. 1983. Comparative water relations of container-grown and bare-root ectomycorrhizal and non-mycorrhizal *Quercus velutina* seedlings. Can. J. Bot. 61: 1559-1565.

Dong, H. and Burdell, A.N. 1986. Chemical root pruning of Chinese pine seedlings raised in cupric sulfide impregnated containers. New For. 1: 67-73.

Dosskey, M.G., Boersma, L., and Linderman, R.G. 1991. Role for the photosynthate demand of ectomycorrhizas in the response of Douglas fir seedlings to drying soil. New Phytol. 117: 327-334.

Duan, X., Neuman, D.S., Reiber, J.M., Green, C.D., Saxton, A.M., and Augé, R.M. 1996. Mycorrhizal influence on hydraulic and hormonal factors implicated in the control of stomatal conductance during drought. J. Exp. Bot. 47: 1541-1550.

Dumroese, R.K. and Wenny, D.L. 1997. An assessment of ponderosa pine seedlings grown in copper-coated polybags. Tree Planters' Notes 48: 60-64.

Duñabeitia, M.K., Hormilla, S., Salcedo, I., and Peña, J.I. 1996. Ectomycorrhizae synthesized between *Pinus radiata* and eight fungi associated with *Pinus* spp. Mycologia 88: 897-908.

Dunn, G.M., Huth, J.R., and Lewty, M.J. 1997. Coating nursery containers with copper carbonate improves root morphology of five native Australian tree species used in agroforestry systems. Agroforest. Syst. 37: 143-155.

Dykstra, P.R. and Curran, M.P. 2000. Tree growth on rehabilitated skid roads in southeast British Columbia. For. Ecol. Manage. 133: 145-156.

Eastman, P.A.K. and Camm, E.L. 1995. Regulation of photosynthesis in interior spruce during water stress: changes in gas exchange and chlorophyll fluorescence. Tree Physiol. 15: 229-235.

Ekwebelam, S.A. and Reid, C.P.P. 1983. Effect of light, nitrogen fertilization, and mycorrhizal fungi on growth and photosynthesis of lodgepole pine seedlings. Can. J. For. res. 13: 1099-1106.

Fleming, L.V., Deacon, J.W., Last, F.T., and Donaldson, S.J. 1984. Influence of propagating soil on the mycorrhizal succession of birch seedlings transplanted to a field site. Trans. Br. Mycol. Soc. 82: 707-711.

Fraser, E.C., Landhäusser, S.M., and Lieffers, V.J. 2003. The effects of mechanical site preparation and subsequent wildfire on trembling aspen (*Populus tremuloides* Michx.) regeneration in central Alberta, Canada. New For. 25: 67-81.

Garbaye, J. and Churin, J.L. 1997. Growth stimulation of young oak plantations inoculated with the ectomycorrhizal fungi *Paxillus involutus* with special reference to summer drought. For. Ecol. Manage. 98: 221-228.

Gingras, B.M. and Richard, S. 1999. On the development of air-slit containers: nursery growth and seedling performance in comparative plantations. Direction de la Recherche Forestiere, Ministere des Ressources Naturelles. Sainte Foy, Quebec. Rep. No. 130.

Gingras, B.M., Richard, S., and Robert, N. 2002. Comparative performance after five years of large sized conifers and broadleaves grown in air-slit containers. Direction de la Recherche Forestiere, Ministere des Ressources Naturelles. Sainte Foy, Quebec. Rep. No. 141.

Girard, S., Clement, A., Cochard, H., Boulet-Gercourt, B., and Guehl, J. 1997. Effects of desiccation on post-planting stress in bare-root Corsican pine seedlings. Tree Physiol. 17: 429-435.

Gomez, A., Powers, R.F., Singer, M.J., and Horwath, W.R. 2002. Soil compaction effects on growth of young ponderosa pine following litter removal in California's Sierra Nevada. Soil Sci. Soc. Am. J. 66: 1334-1343.

Greacen, E.L. and Sands, R. 1980. Compaction of forest soils. A review. Aust. J. Soil Res. 18: 163-189.

Grossnickle, S.C. 1988a. Planting stress in newly planted jack pine and white spruce. 1: Factors influencing water uptake. Tree Physiol. 4: 71-83.

Grossnickle, S.C. 1988b. Planting stress in newly planted jack pine and white spruce. 2: Changes in tissue water potential components. Tree Physiol. 4: 85-97.

Grossnickle, S.C. and Heikurinen, J. 1989. Site preparation: water relations and growth of newly planted jack pine and white spruce. New For. 3: 99-123.

Grossnickle, S.C. and Reid, C.P.P. 1982. The use of ectomycorrhizal conifer seedlings in the revegetation of a high-elevation mine site. Can. J. For. Res. 12: 354-361.

Hagerman, S.H., Jones, M.D., Bradfield, G.E., and Sakakibara, S.M. 1999. Ectomycorrhizal colonization of *Picea engelmannii* × *Picea glauca* seedlings planted across cut blocks of different sizes. Can. J. For. Res. 29: 1856-1870.

Hallsby, G. 1995. Field performance of outplanted Norway spruce: effects of organic matter amendments and site preparation. Can. J. For. Res. 25: 1356-1367.

Halter, M.R., Chanway, C.P., and Harper, G.J. 1993. Growth reduction and root deformation of containerized lodgepole pine saplings 11 years after planting. For. Ecol. Manage. 56: 131-146.

Harvey, A.E., Page-Dumroese, D.S., Jurgensen, M.F., Graham, R.T., and Tonn, J.R. 1997. Site preparation alters soil distribution of roots and ectomycorrhizae on outplanted western pine and Douglas-fir. Plant Soil 188: 107-117.

Heilman, P. 1981. Root penetration of Douglas fir seedlings into compacted soil. For. Sci. 27: 660-666.

Heineman, J. 1998. Forest floor planting: a discussion of the issues as they relate to various site-limiting factors. BC Ministry of Forests, Forest Site Management Section. Victoria, B.C. Silviculture Note 16.

Jansson, K. and Wästerlund, I. 1999. Effect of traffic by lightweight forest machinery on the growth of young *Picea abies* trees. Scand. J. For. Res. 14: 581-588.

Jiang, Y., MacDonald, S.E., and Zwiazek, J.J. 1995. Effects of cold storage and water stress on water relations and gas exchange of white spruce (*Picea glauca*) seedlings. Tree Physiol. 15: 267-273.

Jones, M.D., Durall, D.M., and Cairney, W.G. 2003. Ectomycorrhizal fungal communities in young forests regenerating after clearcut logging. New Phytol. 157: 399-422.

Jones, M.D., Hagerman, S.M., and Gillespie, M. 2002a. Ectomycorrhizal colonization and richness of previously colonized, containerized *Picea engelmannii* does not vary across clearcuts when planted in mechanically site-prepared mounds. Can. J. For. Res. 32: 1425-1433.

Jones, M.D., Kiiskila, S., and Flanagan, A. 2002b. Field performance of pine stock types: Two-year results of a trial on interior lodgepole pine seedlings grown in Styroblocks™, Copperblocks™, or Airblocks™. B.C. J. Ecosys. Manage. 2: 59-70.

Khasa, P.D., Sigler, L., Chakravarty, P., Dancik, B.P., Erickson, L., and McCurdy, D. 2001. Effect of fertilization on growth and ectomycorrhizal development of container-grown and bare-root nursery conifer seedlings. New For. 22: 179-197.

Kranabetter, J.M. and Bulmer, C.E. 1995. Composting trial using pulp fibre waste and municipal sewage sludge. B.C. Min. For. Research Branch, Prince George Forest Region. Prince George, B.C. Forest Science Report.

Kranabetter, J.M. and Osberg, M. 1995. Landing reclamation trials in the Prince George region. B.C. Min. For. Research Branch, Prince George Forest Region. Prince George, B.C. Forest Science Report.

Krasowski, M.J. and Owens, J.N. 2000. Morphological and physiological attributes of root systems and seedling growth in three different *Picea glauca* reforestation stock. Can. J. For. Res. 30: 1669-1681.

Lamhamedi, M., Lambany, G., Margolis, H., Renaud, M., Veilleux, L., and Bernier, P.Y. 2001. Growth, physiology, and leachate losses in *Picea glauca* seedlings (1+0) grown in air-slit containers under different irrigation regimes. Can. J. For. Res. 31: 1968-1980.

Landhäusser, S.M., DesRochers, A., and Lieffers, V.J. 2001. A comparison of growth and physiology in *Picea glauca* and *Populus tremuloides* at different soil temperatures. Can. J. For. Res. 31: 1922-1929.

Lavender, D.P., Parish, R., Johnson, C.M., Montgomery, G., Vyse, A., Willis, R.A., and Winston, D. 1998. Regenerating British Columbia's Forests. UBC Press, Vancouver, B.C.

LoBuglio, K.F. and Wilcox, H.E. 1988. Growth and survival of ectomycorrhizal and ectendomycorrhizal seedlings of *Pinus resinosa* on iron tailings. Can. J. Bot. 66: 55-60.

Lopushinsky, W. and Max, T.A. 1990. Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. New For. 4: 107-124.

Luce, C.H. 1997. Effectiveness of road ripping in restoring infiltration capacity of forest roads. Restor. Ecol. 5: 265-270.

Martin, F., Duplessis, S., Ditengou, F., Largange, H., Vioblet, C., and Layprie, F. 2001. Developmental cross talking in the ectomycorrhizal symbiosis: signals and communication genes. New Phytol. 151: 145-154.

Marx, D.H., Cordell, C.E., and Clark, A.I. 1988. Eight-year performance of loblolly pine with *Pisolithus* ectomycorrhizae on a good-quality forest site. South. J. Appl. For. 12: 275-280.

Marx, D.H., Cordell, C.E., Maul, S.B., and Ruehle, J.L. 1989. Ectomycorrhizal development on pine by *Pisolithus tinctorius* in bare-root and container seedling nurseries I. Efficacy of various vegetative inoculum formulations. New For. 3: 57-66.

Marx, D.H., Ruehle, J.L., Kenney, D.S., Cordell, C.E., Riffle, J.W., Molina, R.J., Pawuk, W.H., Navratil, S., Tinus, R.W., and Goodwin, O.C. 1982. Commercial vegetative inoculum of *Pisolithus tinctorius* and inoculation techniques for development of ectomycorrhizae on container-grown tree seedlings. For. Sci. 28: 373-400.

Mason, E.G. 1985. Causes of juvenile instability of *Pinus radiata* in New Zealand. N. Z. J. For. Sci. 15: 263-280.

Mason, P.A., Ibrahim, K., Ingleby, K., Munro, R.C., and Wilson, J. 2000. Mycorrhizal development and growth of inoculated *Eucalyptus globulus* (Labill.) seedlings in wet and dry conditions in the glasshouse. For. Ecol. Manage. 128: 269-277.

McKay, H.M. 1997. A review of the effect of stresses between lifting and planting on nursery stock quality and performance. New For. 13: 369-399.

McNab, W.H. and Berry, C.R. 1985. Distribution of aboveground biomass in three pine species planted on a devastated site amended with sewage sludge or inorganic fertilizer. For. Sci. 31: 373-382.

McNabb, D.H. 1994. Tillage of compacted haul roads and landings in the boreal forests of Alberta. For. Ecol. Manage. 66: 179-194.

Miller, R.E., Scott, W., and Hazard, J.W. 1996. Soil compaction and conifer growth after yarding at three coastal Washington locations. Can. J. For. Res. 26: 225-236.

Molina, R. 1979. Ectomycorrhizal inoculation of containerized Douglas fir and lodgepole pine seedlings with six isolates of *Pisolithus tinctorius*. For. Sci. 25: 585-590.

Muhsin, T.M. and Zwiazek, J.J. 2002a. Colonization with *Hebeloma crustuliforme* increases water conductance and limits shoot sodium uptake in white spruce (*Picea glauca*) seedlings. Plant Soil 238: 217-225.

Muhsin, T.M. and Zwiazek, J.J. 2002b. Ectomycorrhizas increase apoplastic water transport and root hydraulic conductivity in *Ulmus americana* seedlings. New Phytol. 153: 153-158.

Mukerji, K.G., Chamola, B.P., and Singh, J. 2000. Mycorrhizal Biology. Kluwer Academic, Plenum Publishers, New York, New York. 336p.

Mullin, R.E. 1963. Planting check in spruce. For. Chron. September: 252-259.

Niemi, K., Vuorinen, T., Ernstsen, A., and Häggman, H. 2002. Ectomycorrhizal fungi and exogenous auxins influence root and mycorrhiza formation of Scots pine hypocotyl cuttings in vitro. Tree Physiol. 22: 1231-1239.

Parladé, J., Cohen, M., Doltra, J., Luque, J., and Pera, J. 2001. Continuous measurement of stem-diameter growth response of *Pinus pinea* seedlings mycorrhizal with *Rhizopogon roseolus* and submitted to two water regimes. Mycorrhiza 11: 129-136.

Peng, Y.Y. and Dang, Q.L. 2003. Effects of soil temperature on biomass production and allocation in seedlings of four boreal tree species. For. Ecol. Manage. 181: 1-9.

Phillips, N., Bergh, J., Oren, R., and Linder, S. 2001. Effects of nutrition and soil water availability on water use in a Norway spruce stand. Tree Physiol. 21: 851-860.

Plotnikoff, M.R., Bulmer, C.E., and Schmidt, M.G. 2002. Soil properties and tree growth on rehabilitated forest landing in the interior cedar hemlock biogeoclimatic zone: British Columbia. For. Ecol. Manage. 170: 199-215.

Power, J.F. 1994. An overview of green manures/cover crops. *In* Proc. Northern and inter-mountain forest and conservation nursery association. St. Louis, Mo. Aug 2-5, 1993. *Edited by* T. D. Landis. U.S. Dept. Agric. For. Serv., Fort Collins, Colo. Gen. Tech. Rep. RM-243. pp. 47-52.

Prescott, C.E., Maynard, D.G., and Laiho, R. 2000. Humus in northern forests: friend or foe? For. Ecol. Manage. 133: 23-36.

Qualls, R.G. 2000. Comparison of the behavior of soluble organic and inorganic nutrients in forest soils. For. Ecol. Manage. 138: 29-50.

Quoreshi, A.M. and Timmer, V.R. 2000. Early outplanting performance of nutrient-loaded containerized black spruce seedlings inoculated with *Laccaria bicolor*: a bioassay study. Can. J. For. Res. 30: 744-752.

Radwan, M.A. 1992. Effect of forest floor on growth and nutrition of Douglas-fir and western hemlock seedlings with and without fertilizer. Can. J. For. Res. 22: 1222-1229.

Rajasekaran, L.R. and Blake, T.J. 1998. Early growth invigoration of jack pine seedlings by natural plant growth regulators. Trees 12: 420-423.

Rietveld, W.J. 1989. Transplanting stress in bareroot conifer seedlings: its development and progression to establishment. North. J. Appl. For. 6: 99-107.

Ritchie, G.A. and Dunlap, J.R. 1980. Root growth potential: its development and expression in forest tree seedlings. N. Z. J. For. Sci. 10: 218-248.

Roberts, J. 1996. Understanding Soil Mechanics. Delmar Publishers, Albany, N.Y. 255p.

Roth, A.L. and Berch, S.M. 1992. Ectomycorrhizae of Douglas fir and western hemlock seedlings outplanted on eastern Vancouver Island. Can. J. For. Res. 22: 1646-1655.

Ruehle, J.L. 1985. The effect of cupric carbonate on root morphology of containerized mycorrhizal pine seedlings. Can. J. For. Res. 15: 586-592.

Runion, G.B., Mitchell, R.J., Rogers, H.H., Prior, S.A., and Counts, T.K. 1997. Effects of nitrogen and water limitation and elevated atmospheric CO_2 on ectomycorrhiza of longleaf pine. New Phytol. 137: 681-689.

Sahlén, K. and Goulet, F. 2002. Reduction of frost heaving of Norway spruce and scots pine seedlings by planting in mounds or in humus. New For. 24: 175-182.

Sanborn, P., Bulmer, C., Coopersmith, D., and Erikson, D. 1999. Soil rehabilitation research at the Aleza Lake research forest: Techniques for restoring productivity to fine-textured soils. B.C. Ministry of Forests. Victoria, B.C. Forest Research Note. PG-18.

Scagel, C.F. and Linderman, R.G. 2001. Modification of root IAA concentrations, tree growth, and survival by application of plant growth regulating substances to container-grown conifers. New For. 21: 159-186.

Schmidt, M.G., MacDonald, S.E., and Rothwell, R.L. 1996. Impacts of harvesting and mechanical site preparation on soil chemical properties of mixed-wood boreal forest sites in Alberta. Can. J. Soil Sci. 76: 531-540.

Simard, S.W., Jones, M.D., Durall, D.M., Hope, G.D., Stathers, R.J., Sorensen, N.S., and Ziomonick, B.J. 2003. Chemical and mechanical site preparation: effects on *Pinus contorta* growth, physiology, and micro-site quality on steep forest sites in British Columbia. Can. J. For. Res. 33: 1495-1515.

Simard, S.W., Perry, D.A., Smith, J.E., and Molina, R. 1997. Effects of soil trenching on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. New Phytol. 136: 327-340.

Smethurst, P.J. 2000. Soil solution and other analyses as indicators of nutrient supply: a review. For. Ecol. Manage. 138: 397-411.

Smith, S. E. and Read, D. J. 1987. Mycorrhizal Symbiosis. Academic Press. San Diego, California. 605p.

South, D.B. and Zwolinski, J.B. 1997. Transplant stress index: a proposed method of quantifying planting check. New For. 13: 315-328.

Stowe, D.C., Lamhamedi, M.S., and Margolis, H.A. 2001. Water relations, cuticular transpiration, and bud characteristics of air-slit containerized *Picea glauca* seedlings in response to controlled irrigation regimes. Can. J. For. Res. 31: 2200-2212.

Sutherland, B. and Foreman, F.F. 2000. Black spruce and vegetation response to chemical and mechanical site preparation on a boreal mixedwood site. Can. J. For. Res. 30: 1561-1570.

Sutton, R.F. 1991. Soil properties and root development in forest trees: A review. Forestry Canada. Sault Ste. Marie, Ont. Information Report O-X-413.

Valdés, M. 1986. Survival and growth of pines with specific ectomycorrhizae after 3 years on a highly eroded site. Can. J. Bot. 64: 885-888.

van den Driessche, R. 1987. Importance of current photosynthate to new root growth in planted conifer seedlings. Can. J. For. Res. 17: 776-782.

van Rees, K. and Jackson, D. 2001. Impacts of ripping and rollback of organic matter on landings and roadways in harvested blocks in central Saskatchewan. Prince Albert Model Forest Association. Saskatoon, SK. Final Report. 36p.

Vyse, A.H., Birchfield, G.A., and van Eerden, E. 1971. An operational trial of the styroblock reforestation system in British Columbia. Environ. Can., Can. For. Serv. Victoria, B.C. Inf. Rep. BC-X-59.

Walker, R.F. 1999. Reforestation of an eastern Sierra Nevada surface mine with containerized jeffrey pine: seedling growth and nutritional responses to controlled release fertilization and ectomycorrhizal inoculation. J. Sustain. For. 9: 127-147.

Walker, R.F. and Kane, L.M. 1997. Containerized jeffrey pine growth and nutrient uptake response to mycorrhizal inoculation and controlled release fertilization. West. J. Appl. For. 12: 33-40.

Wan, X., Landhäusser, S.M., Zwiazek, J.J., and Lieffers, V.J. 1999. Root water flow and growth of aspen (*Populus tremuloides*) at low root temperatures. Tree Physiol. 19: 879-884.

Williamson, J.R. and Neilsen, W.A. 2000. The influence of forest site on rate and extent of soil compaction and profile disturbance of skid trails during ground-based harvesting. Can. J. For. Res. 30: 1196-1205.

Wu, B., Watanabe, I., Hayatsu, M., and Nioh, I. 1999. Effect of ectomycorrhizae on the growth and uptake and transport of ^{15}N-labelled compounds by *Pinus tabulaeformis* seedlings under water-stressed conditions. Biol. Fert. Soils 28: 136-138.

Chapter 2

Growth of (1+0) *Pinus contorta* var. *latifolia* seedlings produced in different container types and planted on rehabilitated landings, tilled landings, and cutblocks

Introduction

Ground based forestry operations typically necessitate the construction of haul roads, skid trails, and log landings. Construction and subsequent usage of landings acts to severely alter the soil in these locations. Landings are constructed by scraping away surface soil horizons followed by cutting of subsoil and filling to level the site. This removal of upper soil horizons results in depressed seedling growth due to the displacement of nutrients and organic matter from the landing (Radwan 1992; Prescott *et al.* 2000; Gomez *et al.* 2002).

Landing construction and subsequent heavy machine traffic, including loaded log trucks, also results in compaction of soil (Jansson & Wästerlund 1999). Depending upon the soil and site characteristics, soil compaction may significantly increase landing soil bulk density (Carr 1988) to the level where tree growth is substantially reduced (Bulmer 1998). Soil compaction negatively affects infiltration rates, soil structure, and water movement (Sutton 1991; Miller *et al.* 1996). Furthermore, compaction adversely affects seedling root growth and root system development via mechanical impedance (Senyk & Wass 1999). This, in turn, results in low root to shoot ratios, low shoot mineral status, and poor seedling growth for many years following planting (Greacen & Sands

1980; Conlin & Van den Driessche 1996). Thus, landings are typified by nutrient poor compacted soils and low plant productivity (Bulmer 1998).

Rehabilitation of log landings has been attempted via various methods in the past, with different attempts to restore site productivity. Alleviation of compacted soils (McNabb 1994; Luce 1997; Bulmer 2000), and restoration of soil nutrients by various methods (Bauhus & Meiwes 1994; Kranabetter & Bulmer 1995; Kranabetter & Osberg 1995), have provided mixed results. However, successful landing rehabilitation has been reported (Plotnikoff *et al.* 2002). Although various methods have resulted in successful rehabilitation (Bulmer 2000), implementation of such methods has been restricted due to the additional costs involved as a result of the characteristics of landings once harvesting operations cease, as well as the logistics of the implementation of these methods.

The present project was developed to assess landing rehabilitation methods that utilize materials found on site, thereby keeping additional expenditure at a minimum. I evaluated the incorporation of topsoil, which had been removed during landing construction and stockpiled on site, and burn-pile debris (burned slash) via mechanical tillage, on the growth and performance of planted interior lodgepole pine seedlings. Seedlings were grown in Styroblocks™, Copperblocks™, and AirBlocks™, some of which had been inoculated with ectomycorrhizal fungi, in order to determine whether these nursery treatments influenced seedling response to landing treatments. I hypothesized that rehabilitation of log landings, by mechanical tilling and incorporating recovered topsoil and burn-pile debris, would alleviate soil compaction and restore site productivity to levels equal with the adjacent cutblock. Particular focus was upon seedling growth rates, root emergence, and seedling mycorrhizal status.

Materials and Methods

Study Site

Seedlings were planted into three replicate landings in a 20.3-hectare cutblock in the Will Lake area of the southern interior of British Columbia (near Falkland, BC, 50°27.17N, 119°38.33W, 1244 m asl, Figure 2-1). The study area is located in the Interior Douglas-fir biogeoclimatic zone, Cascade dry cool variant, site series 03 (IDF dk2 03) (Pojar *et al.* 1987; Lloyd *et al.* 1990). The underlying mineral soil has loam to sandy loam texture, contains up to 20% coarse fragments, and is overlain with a 3-cm layer of moder humus. Coarse-textured soils in the area are classified as Orthic Eutric Brunisols, while medium- and fine-textured soils are classified as Orthic Gray Luvisols (Soil Classification Working Group, 1998). Located on the northeastern edge of the Thompson Plateau, this site is classified as submesic to subxeric with mean annual precipitation of 568 mm, and cool, with a mean daily temperature of 4.1°C (Reynolds 1989). Shrub and herbaceous vegetation in the cutblock consisted of falsebox (*Paxistima myrsinites*) and soopolallie (*Shepherdia canadensis*), with a significant majority of the ground cover consisting of pinegrass (*Calamagrostis rubescens*). This cutblock had been clearcut logged in February 1999, to prevent the spread of Mountain Pine Bark Beetle, and operationally planted the following spring.

Nursery treatments

One-year-old (1+0) interior lodgepole pine (*Pinus controrta* var. *latifolia*) seedlings (seedlots 10828 and 32720) were produced at Pacific Regeneration Technology (PRT) Vernon Nursery, Vernon, British Columbia. Seedlings were grown in new Styroblocks™ (PSB 410, 80 ml, Beaver Plastics Ltd., Edmonton, Alberta), Copperblocks™ (PCT 410, 80 ml, Beaver Plastics Ltd.), or AirBlocks™ (PAB 410, 80 ml, BCC Silviculture Technology, Landskrona, Sweden). Randomly selected blocks of each type were inoculated with one of two fungal inocula: a mycelial slurry of *Hebeloma longicaudum* (Pers.:Fr.) Kummer (Mikro-Tek Inc., Timmins, Ontario), a spore slurry of *Rhizopogon rubescens* Tul. (Mycorrhizal Applications Inc., Grants Pass, Oregon), or left as non-inoculated controls. Ectomycorrhizal fungal inoculum was diluted seven-fold with water, and applied with a watering can, as per supplier recommendations. Seedlings were inoculated once with *H. longicaudum* (July 28, 1999) and twice with *R. rubescens* (July 16 and October 5, 1999). Seedlings were grown to target morphological parameters for commercially planted pine seedlings of that stock type in British Columbia: 14 cm for height and 3.2 mm for root collar diameter. All seedlings, except those grown in AirBlocks™, met the minimum height (7 cm) and diameter (2.5 mm) specifications (stem volume index at lifting derived from height and diameter, Table 2-1). Seedlings were sown in the spring of 1999, lifted in December 1999, and frozen stored at -2°C. Seedlings were planted out during the first week of June 2000.

During lifting, a random sample of seedlings from each combination of container type and fungal inoculation treatment was selected for initial morphological

measurements, quantification of ectomycorrhizal colonization, and assessment of root emergence. The height, root collar diameter, and mycorrhizal colonization were quantified on eight seedlings per nursery treatment. A random sample of 50 live root tips from the outer surface of each root plug was examined under a light microscope (70x and 400x magnification). Root tips were classified as ectomycorrhizal if a mantle was present. To study seedling root emergence patterns eight seedlings per nursery treatment were individually transplanted into 10×25 cm pots containing a sand/peat/vermiculite mixture (2:1:1 by volume) and grown for 10 days at 24°C with a 16 h photoperiod of 400 μmol m^{-2} s^{-1} PAR. Watering was to the point of runoff every three days. After harvest, the number of new emergent white roots greater than 1 cm in length was counted in three sections of the root plug (top third, middle third, bottom third).

Seedling Planting

Experimental seedlings were planted into three replicate sites. Each site encompassed three plots, each with a different rooting environment: two landing rehabilitation treatments and the adjacent cutblock. In October 1999, landings were tilled to a depth of 50 cm with a rock ripper attached to a crawler tractor. Prior to mechanical tilling, recovered topsoil, which had been scalped during landing construction, was spread over one half of each landing. Associated with the recovered topsoil were varying amounts of ash, charcoal, and partially burned wood, which resulted from disposal of logging slash that had accumulated in the vicinity of the landings during the operational harvesting and log loading operations. Division of the landings into two halves, and

selection of the subsequent applied rehabilitation treatment, was dependant upon the location of the burnpile and stockpiled topsoil. Landing rehabilitation treatments were separated by a 5 m wide control strip, across the centre of the landings, where seedlings were not planted. During the first week of June 2000, approximately 40 seedlings from each of the nine nursery treatments (container type × fungal inoculum) were randomly planted at 1 m spacing, into each plot (approximately1080 seedlings per site).

Growth in the Field

Seedling growth was assessed at the end of each of the first two growing seasons (October 2000 and October 2001). Twenty seedlings of each of the 27 nursery treatment / rooting environment combinations (three container types × three inoculation treatments × three rooting environments), from each site, were randomly selected for measurements in 2000. The same seedlings were measured again in 2001. Seedling height and diameter were used to determine seedling stem volume index (V).

[1] $$V = d^2 h$$

Where d is the stem ground level diameter and h is the seedling height from ground level to the tip of the terminal bud. Seedling growth was determined by the calculation of absolute growth rates (G), or the incremental change in seedling volume between the second season and the first season (Hunt 1982).

[2] $$G_{1-2} = \frac{V_2 - V_1}{T_2 - T_1}$$

Where V is seedling stem volume (equation [1]) and T is the time interval (growth season). To ascertain seedling growth rates over the first field season irrespective of initial seedling volume and over the second field season irrespective of volume at the end of the first season, seedling relative growth rates (R) were calculated (Hunt 1982).

[3] $$R_{1-2} = \frac{\log_e V_2 - \log_e V_1}{T_2 - T_1}$$

Where V is seedling stem volume (equation [1]) and T is the time interval (growth season). Seedlings were also assessed for vigour at the end of the second season (2001), with seedlings assigned a number, from 0 to 3, based upon their growth, form, and survival (0-dead; 1-poor appearance, chlorotic and stunted, not likely to survive, minimal growth; 2-average seedling, green and healthy, average growth and form; 3- robust large seedling, lush green and healthy, excellent growth and form).

After two seasons of growth in the field a random sample of eight seedlings from each of the 27 treatments was harvested per site to assess seedling growth parameters (shoot dry mass, root dry mass, seedling dry mass, root to shoot ratio, and root emergence patterns) and ectomycorrhizal status of roots. Root emergence pattern was determined by counting the number of roots greater than 1 cm in length emerging from the top, middle, and bottom thirds of the root plug. Subsequent to root emergence

assessment, root plugs were washed to remove all soil and debris, and air-dried. Root plugs and stems were oven dried to a constant mass at 60°C and weighed.

Mycorrhizal Status

Root plugs were soaked in water and the roots were gently cleaned free of soil and debris. All roots, including those in the root plugs, were cut into approximately 2 cm pieces. All root tips on randomly selected root pieces were examined, until 200 root tips per seedling had been classified (minimum of 1200 root tips per container × inoculum × rooting environment treatment per site: 32,400 root tips per site). Ectomycorrhizae were classified into morphological types using the method of Goodman *et al.* (1996) and compared to descriptions published in Agerer (1987-2000) and Ingleby *et al.* (1990). Characteristics such as root branching patterns, root tip colour, surface texture and lustre, were determined under a stereomicroscope (40x). Hyphal pattern of the inner and outer mantle as well as surface features, such as cystidia, presence or absence of extramatrical hyphal clamps, extramatrical hyphal ornamentation and colour, were determined on whole root mounts or mantle peels (fungal tissue only) under the light microscope (400x or 1000x). Mantle peels were made by gently separating fungal tissue from root tissue using fine forceps and a hypodermic needle. Both dead root tips and root tips that were not colonized by ectomycorrhizal fungi were characterized as non-mycorrhizal. Root tips exhibiting early stages of fungal colonization (such as incomplete mantle formation) were classified as 'incomplete'.

Simpson's reciprocal index of diversity ($1/D$) was used to determine the diversity of the ectomycorrhizal community present on seedling roots (Krebs 1999).

[4] $$\frac{1}{D} = \frac{1}{\sum p_i^2}$$

Where $1/D$ is Simpson's reciprocal index (varies from 1 to the number of morphotypes found in the sample), and p_i is the proportion of morphotype i in the community. Ectomycorrhizal community equitability was expressed as Simpson's measure of evenness (E), which follows from Simpson's measure of diversity (Krebs 1999).

[5] $$E_{1/D} = \frac{1/D}{s}$$

Where $1/D$ is Simpson's reciprocal index (equation [4]), and s is the number of ectomycorrhizal morphotypes in the sample. Simpson's indices of diversity and evenness were chosen because they are relatively unaffected by rare ectomycorrhizal morphological types in the sample. The percentage of roots colonized was calculated as the total number of active ectomycorrhizal root tips divided by the total number of root tips examined. Relative abundance was calculated as the number of ectomycorrhizal root tips of each morphotype, as a proportion of the total number of root tips examined per seedling. Ectomycorrhizal richness was calculated as the total number of morphotypes,

including those classified as incomplete. Percent colonization, richness, diversity, and evenness, were determined on an individual seedling basis.

Soil Analyses

Soil bulk density was determined on intact soil cores (Blake & Hartge 1986) collected using a drop-hammer sampler and a 0.52 l core. At each of five random sampling points per plot, a core was taken from the 0-7 cm depth and an additional core was taken at 10-17 cm depth. Soil samples for bulk density determination were dried and coarse fragments (diameter >2 mm) sieved out and weighed. Mineral coarse fragments were assumed to have a particle density of 2600 kg m^{-3}. Fine fraction soil bulk density was calculated as the mass of dry, coarse-fragment-free mineral soil per volume of field-moist soil, where volume was also calculated on a coarse-fragment-free basis.

The sieved soil samples obtained for the bulk density determination were subsequently analyzed for total C and N, mineralizable N, soil pH, available P, cation exchange capacity (CEC), and exchangeable K, Ca, and Mg, by the British Columbia Ministry of Forests Research Branch laboratory, Victoria B.C. Total soil C and N were determined by a dry combustion method (Nelson & Sommers 1982) using a Fisons NA-1500 analyzer. Mineralizable N was determined from ammonium-N in a KCl extract of soil following a two-week anaerobic incubation at 30°C (Bremner 1996). The soil pH was determined on a 1:2 (v/v) soil to distilled water slurry (McLean 1982). Available P was determined by extraction with ammonium fluoride and hydrochloric acid (Kalra &

Maynard 1991). Soil CEC and exchangeable K, Ca, and Mg, were determined by extraction with barium chloride (Hendershot & Duquette 1986). Results from the chemical analysis are reported on an oven-dry weight basis.

At each of ten random sampling locations per plot, soil mechanical resistance (Bradford 1986) was measured in May and June 2002 at 10 cm depth using a hand-pushed cone penetrometer with a 4 mm cone tip. Similarly, volumetric soil water content at 10 cm depth was determined in May and June 2002 with a theta probe (Delta-T Devices 1999). Soil particle size distribution was determined by the hydrometer method (Gee & Bauder 1986) on samples taken at 0-7 and 10-17 cm depths.

Soil temperature at the bottom of the root plug, was determined using Hobo Temp data loggers (Onset Computer Co., Pocasset, Massachusetts, USA). Data loggers, three per landing, were located at the center of each plot, and buried in sealed containers at a depth of 10 cm. Data loggers recorded soil temperature three times daily (00:00, 08:00, 16:00) from October 2000 through June 2002. The minimum soil temperature below which root growth did not occur was assumed to be 3.5°C (Sutton 1991). Consequently, the length of the growing season was determined by counting the number of days where minimum daily soil temperature remained consistently above 3.5°C. Results of soils analysis are presented to encompass the rooting zone (0-17 cm depth), with the mean value between cores (0-7 cm and 10-17 cm) presented.

Experimental Design and Data Analysis

All seedling variables were analyzed with respect to each of the following factors in a completely randomized full factorial design: site, container type, fungal inoculum, and rooting environment. Soil chemical and physical property variables were similarly analyzed with respect to site, soil treatment, and soil depth. Soil temperature data was analyzed with respect to site and rooting environment. Due to the fact that 'site' was not a properly replicated variable, with no replication within each site, site effects will not be discussed further. Prior to statistical analysis, seedling and soil property data were examined to ensure assumptions of a multivariate analysis of variance were met (Steel *et al.* 1997; Tabachnick & Fidell 2001). All seedling and soils data were analyzed using the general linear model multivariate analysis of variance (SPSS version11.5, SPSS Inc. Chicago IL; SAS version 8.0, Cary, NC). Soil temperature data was similarly analyzed using the general linear model univariate analysis of variance. Separation of significant main effect mean values was based upon an honestly significant difference using Tukey's *W* procedure, while multiple pairwise comparisons (Bonnferroni), were used to separate treatment interactions, with the significance level interpreted as $p<0.05$. The means presented are overall estimated marginal mean values.

The two seedlots (10828 and 32720) used in this study were combined for the purpose of analysis. Initial stock quality assessments (root growth capacity, viability testing, drought stress tolerance, total non-structural carbohydrate content of roots and shoots) revealed no significant differences between seedlots with respect to any variable

(Appendix I). All results reported here represent means derived from pooled data consisting of an equal number of samples from each seedlot.

Results

Initial Seedling Morphology

During lifting a random sample of seedlings from each nursery treatment (container × fungal inoculum) was evaluated for seedling volume index (Table 2-1). Seedlings grown in Copperblocks™ and Styroblocks™ were at least 34% larger at lifting, than seedlings grown in AirBlocks™ (p<0.001). Fungal inoculation did not affect seedling size in the nursery (p=0.3). During growth in the nursery approximately 45% of non-inoculated seedling root tips became colonized with ectomycorrhizal fungi (Table 2-1). Although container type and fungal inoculation did not affect colonization rates, a significant interaction was noted between treatments, with AirBlock™/*H. longicaudum* and Styroblock™/*R.. rubescens* root systems exhibiting substantially higher colonization rates (p<0.001, 73 ± 8% and 79 ± 9% respectively).

Container type also elicited significant differences in emergent root growth at lifting (Table 2-2). Copperblock™ seedlings produced approximately 52% more new roots, than did AirBlock™ and Styroblock™ seedlings (p=0.004). New roots emerged in different arrangements: Copperblock™ and AirBlock™ seedlings produced a greater proportion of roots from the top portion of the root plug than Styroblock™ seedlings (p<0.001). Fungal inoculation also resulted in significant differences in the number of

new emergent roots produced from the root plug at lifting (p=0.005, Table 2-2). Non-inoculated control seedlings produced the greatest number of emergent roots, 28% more than did *Hebeloma*-inoculated seedlings, and 64% more than *Rhizopogon*-inoculated seedlings. Fungal inoculation did not affect the distribution of new emergent roots (p>0.3). A significant interaction was found between container type and fungal inoculum (Table 2-2), as non-inoculated Copperblock™ seedlings produced substantially more new roots (118.5 ± 10.0), than did all other inoculation-container combinations (average of 48.2 ± 9.5).

Growth in the Field

By the end of the second growing season, seedlings planted onto the portions of landings that had been rehabilitated with topsoil and burn-pile debris had greater root dry mass and stem volume than seedlings planted on the other portion of the landings or on the cutblock (p<0.001, Table 2-1). By this time, shoots of seedlings on fully rehabilitated landings had two-fold greater dry mass and 60% greater stem volume index compared with those planted in the cutblock (Table 2-1). Stem volume index of seedlings planted on the tilled-only sides of the landings were only 41 % of those on the fully rehabilitated side. Root to shoot ratios were not affected (p=0.7, Appendix I). Significant differences in seedling size were due to differences in absolute and relative growth rates. Seedlings planted on fully rehabilitated landings exhibited greater relative growth (Figure 2-2A, p<0.001) and greater absolute growth rates (Figure 2-2B, p<0.001) than seedlings planted in the cutblock, with seedlings planted on tilled-only landings demonstrating the

lowest growth rates. Seedlings planted on fully rehabilitated landings were ranked as being healthier and more robust, than seedlings either on the cutblock or on tilled landings (p=0.001, Table 2-1).

Seedlings grown in different container types differed in stem volume index after both growing seasons (p<0.001, Table 2-1). Following the first season of field growth Copperblock™ seedlings were 20% larger than Styroblock™ seedlings, and 73% larger than AirBlock™ seedlings. Subsequent to the second season of field growth, Copperblock™ seedlings were still largest by approximately 59%, however AirBlock™ seedlings were now approximately equal in volume index to Styroblock™ seedlings. Changes in respective seedling stem volume index were due to differences in relative growth rates. The AirBlock™ seedlings, although substantially smaller than the other seedlings at lifting, exhibited the same relative growth rates as Copperblock™ seedlings and both of these had higher relative growth rates than Styroblock™ seedlings (Figure 2-3A, p<0.001). The Copperblock™ seedlings had higher absolute growth rates than the other seedlings even though they were similar in volume to Styroblock™ seedlings at lifting (Figure 2-3B, p<0.001). Differences in growth rates between container types across the different rooting environments, also resulted in a significant interaction with respect to stem volume index after both the first and second season (Table 2-1). Although significant, the same general relationship amongst container types, as seen with growth rates, was observed in stem volume index, with differences emerging due to the fact that seedlings on landings that received topsoil and burn-pile debris were substantially larger. After two seasons, Copperblock™ seedlings on fully rehabilitated landings were 62% larger than AirBlock™ and Styroblock™ seedlings. Differences

were smaller on tilled landings and in the cutblock, where both Copperblock™ and Styroblock™ seedlings were marginally larger than AirBlock™ seedlings. Root mass of AirBlock™ seedlings were still substantially lower than the other seedlings after two field seasons ($p = 0.04$, Table 2-1), but shoot mass, root to shoot ratio (Appendix I), and seedling vigour assessment, were not affected by container type.

Fungal inoculation did not result in any significant differences in seedling size, vigour (Table 2-1) or growth rates (Appendix I) after two field seasons. A significant interaction was found between fungal inoculum and rooting environment (Table 2-1), as seedlings inoculated with *H. longicaudum* exhibited greater whole seedling dry mass than non-inoculated seedlings, only when planted on tilled landings. Seedlings produced the same number of new emergent roots in the field regardless of nursery treatment or rooting environment (Table 2-2). Seedlings from all treatments produced approximately 50 emergent roots, with approximately 11% from top of plug, 22% from the middle, and 68% from the bottom of the plug. Rooting environment and container type resulted in a significant interaction (Table 2-2) with respect to the proportion of emergent roots produced from the top of the root plug. Styroblock™ seedlings on fully rehabilitated landings produced 48% less root growth from the top portion of the root plug than did AirBlock™ and Copperblock™ seedlings.

Mycorrhizal Status

I observed 21 distinct morphological types of ectomycorrhizae on approximately 97,200 root tips sampled from the Will Lake sites (Appendix III). Twelve of the 21

morphotypes occurred on more than 1% of sampled root tips (Figure 2-4). Rooting environment significantly affected colonization by ectomycorrhizal fungi (Figure 2-4A). Seedlings planted in the cutblock were colonized with ectomycorrhizal fungi to a greater extent than were seedlings planted either on rehabilitated landings or tilled landings ($p<0.001$). These seedlings formed a higher proportion of MRA (*Mycelium radicis atrovirens*) ($p=0.03$), *Hebeloma*-like 1 ($p<0.001$), and *Hebeloma*-like+MRA ($p<0.001$) ectomycorrhizae, than other seedlings. A higher percentage of roots on fully rehabilitated landings formed E-Strain 1 mycorrhizae ($p=0.04$), while conversely the relative abundance of the *Laccaria*-like type was reduced ($p=0.048$) when compared to seedlings on tilled landings. Root systems of seedlings in the cutblock also exhibited greater ectomycorrhizal richness ($p<0.001$, Figure 2-5C), diversity, ($p<0.001$, Figure 2-5B), and evenness ($p=0.005$, Figure 2-5A). Seedlings were colonized with an average of 2.5 ± 0.16 morphological types.

Container type did not affect ectomycorrhizal colonization or the relative abundance of the major morphotypes ($p=0.3$, Figure 2-4B). Container type did, however, affect ectomycorrhiza richness ($p=0.001$, Figure 2-6C): there was an average of 3.0 morphological types on each AirBlock™ and Styroblock™ seedling, but only 1.3 types per Copperblock™ seedling. Neither ectomycorrhizal diversity ($p=0.3$, Figure 2-6B) nor ectomycorrhizal evenness ($p=0.6$, Figure 2-6A) was significantly affected by container type after two seasons growth in the field.

Inoculation with ectomycorrhizal fungi significantly affected the ectomycorrhizal colonization ($p=0.01$, Figure 2-4C) of seedling root systems. Both non-inoculated and seedlings inoculated with *H. longicaudum* were colonized to a greater extent than

seedlings inoculated with *R. rubescens*. Additionally, seedlings inoculated with *H. longicaudum* showed increased relative abundance of both the *Hebeloma*-like 2 (p=0.02) and *Hebeloma*-like 3 morphotypes (p=0.049). Although inoculation did not significantly affect ectomycorrhizal richness (p=0.09, Figure 2-7C) or diversity (p=0.7, Figure 2-7B), evenness was highest in seedlings inoculated with *H. longicaudum* (p=0.02, Figure 2-7A) likely due to the increased relative abundance of five morphological types (incomplete, MRA, *Hebeloma*-like 2, E-Strain 1, *Hebeloma*-like 3). Richness of *H. longicaudum* inoculated seedlings tended to be lower than *R. rubescens* and control seedlings.

Soil Properties

Untreated soils, from landing control strips, and those that were simply tilled had higher soil bulk density than plots receiving topsoil or cutblock sites (Table 2-3). Landing plots receiving topsoil had higher total carbon, total nitrogen, and available phosphorus than plots that were simply tilled (Table 2-4). Bulk density was strongly influenced by carbon content (Figure 2-8, R^2=0.67, p<0.001). Mineralizable N values were highest for cutblock soils. Soil pH values for the plots receiving topsoil were higher, and those from the cutblock were lower, than those for the tilled or untreated landing soils

Soil resistance for tilled plots, and those receiving topsoil were considerably lower than for untreated control portions of the landing (Figure 2-9, p<0.001), and were equal to the cutblock plots in May. Soil mechanical resistance, as expected, was not

within the growth-limiting range in spring, but values increased as the soils dried from May to June, and likely continued to increase in July and August as soils were affected by summer moisture deficits. A large increase in soil resistance for the cutblock soils in June coincided with a large decrease in soil moisture levels during that period (Figure 2-9). Although plots receiving topsoil experienced similar moisture levels to cutblock plots in June, mechanical resistance was the lowest of all plots (p=0.009).

Landing plots experienced significantly warmer soil temperatures at a depth of 10 cm (p<0.001, Figure 2-10) than cutblock plots. Plots receiving topsoil and burn-pile debris warmed up earlier in the spring, and cooled down later in the fall, than did tilled plots and the adjacent cutblock. Addition of topsoil and burn-pile debris to landing plots resulted in an increase in the growing season, over the adjacent cutblock as well as tilled plots (p=0.03). During the second season of seedling growth (2001), fully rehabilitated landing plots exhibited 176 ± 2 days where the minimum daily soil temperature was above 3.5°C, while cutblock soils and tilled soils showed fewer days above 3.5°C (163 ± 4 and 162 ± 4 respectively). Over the two seasons of study, rehabilitated landings experienced an increased mean daily soil temperature over both other plots (7.10 ± 0.04°C, p<0.001) while tilled plot soils (6.82 ± 0.04°C) were warmer than cutblock soils (5.91 ± 0.04°C).

Discussion

Container Type

In British Columbia, there are presently two container types commonly used for the commercial production of conifer seedlings (i.e. Styroblocks™ and Copperblocks™), while AirBlocks™ account for only a small portion of commercial production. In the present study, both Copperblock™ and Styroblock™ stock surpassed AirBlock™ stock in terms of seedling volume index during growth in the nursery; however, differences in seedling size at lifting were most likely attributable to the irrigation regime and not to container effects per se. All stock types received the same amount of water in the nursery even though, due to their hard plastic air-slit design, AirBlocks™ require more water than other stock types. In a similar study, AirBlock™ seedlings were supplied with adequate irrigation, and did not differ in size from the other stock types (Chapter 3).

The standard styrofoam block style container provides an affordable means of seedling propagation; however, concerns over root emergence patterns (Balisky *et al.* 1995) and possible future stand stability (Mason 1985; Burdett *et al.* 1986) lead to modifications, such as addition of ribs to the interior walls, of the standard container (e.g. Styroblock™). Additionally, further modifications of container design allow for both chemical root pruning (e.g. Copperblock™) and air root pruning (e.g. AirBlock™) of nursery stock. Both Copperblocks™ and AirBlocks™ achieve root pruning in essentially the same way. Lateral roots contact the container walls and cease growing, thereby promoting the growth of new lateral roots (Arnold & Struve 1993) and resulting in a

consistently diffuse fibrous root plug (Lamhamedi *et al.* 2001). In this study, root emergence patterns in the growth chamber varied amongst stock types as expected. Copperblock™ seedlings produced more new roots in total, as well as a greater percentage of roots from the top of the plug, while AirBlock™ seedlings produced a greater percentage of roots from the middle and top of the plug.

Root growth potential has been correlated with the field performance of *Pinus contorta* (Simpson 1990) and, therefore, is widely used as an indicator of seedling quality (Simpson & Vyse 1995). However, assessment of the root growth potential of nursery stock can be affected considerably by the test conditions (Simpson & Ritchie 1997). Seedlings outplanted at the Will Lake sites were exposed to conditions very much different than those potted in a growth chamber (e.g. available water, soil temperature). Therefore, it is not surprising that the results in the field did not mimic those from the lab prior to planting. In the field container type did not affect root emergence patterns and, although Copperblock™ and Styroblock™ root systems were of greater mass after two seasons growth, this difference in root mass was most likely a remnant of the differences in seedling size at lifting. Many studies provide evidence that root pruning, hence potentially container type, affects the initial root form of planted seedlings (Dong & Burdell 1986; Arnold & Struve 1989; Dunn *et al.* 1997; Aldrete *et al.* 2002); however, it is not clear whether longer term growth is affected. Although Styroblock™ seedlings planted on landings receiving topsoil and burn-pile debris produced less new emergent root growth from the top of the root plug, results here indicate that the initial influence of container type on root emergence patterns can potentially disappear within two growing seasons in the field. This may be because after outplanting, root growth potential is

influenced highly by plantation environmental factors (Ritchie & Dunlap 1980). This study provides evidence that site conditions moderate root growth to a much greater extent than nursery treatments, even after only two growing seasons in the field.

While growth in the nursery is important, growth and performance of seedlings after outplanting is of ultimate importance for successful reforestation. My results suggest that root pruning influences the early above ground growth of outplanted seedlings (i.e., 1-2 years), and if trends continue, will have a significant effect upon longer-term growth (i.e. 3+ years). Copperblock™ seedlings were larger than the others at lifting and continued to have higher absolute growth rates throughout the study. Relative growth rates were also higher than Styroblock™ seedlings. These results are consistent with those of Aldrete *et al.* (2002) who, as a result of a recent greenhouse study, predicted that copper-treated *Pinus pseudostrobus* and *P. montezumae* would show increased survival and growth in the field, due to their increased seedling size and root morphology at lifting. The present results also agree with Burdett *et al.* (1983), who found that copper-pruned *Pinus contorta* were 15% taller after 4 years growth in the field. Conversely, other studies of copper-treated stock have not demonstrated significantly greater survival and growth of lodgepole pine seedlings (Burdett 1981; Clarke & Winter 1987), or have found only marginal increases (Clarke & Winter 1986; Winter & Low 1990). Similar comparisons using *Pinus monticola*, *P. ponderosa*, and *Pseudotsuga menziesii*, also found no significant above ground growth responses (Wenny 1988). There is also a lack of evidence to suggest that copper-treated lodgepole pine stock is less susceptible to toppling. Krasowski *et al.* (1996) concluded that factors

such as stocking density and soil properties are more responsible for stand stability, than stock type.

Air pruning of seedling roots significantly affects initial root morphology and early growth (Gingras & Richard 1999; Lamhamedi *et al.* 2001; Gingras *et al.* 2002); however, little is known regarding post planting growth response. In a recent study, Gingras *et al.* (2002) report similar root development, growth, and survival, of air-slit grown (i.e. AirBlock™) *Picea mariana* and *P. glauca*, 5 years after planting when compared to seedlings grown using conventional containers. In the present study, AirBlock™ seedlings, although considerably smaller at planting, exhibited high relative growth rates, and after the second season were not significantly different in size from Styroblock™ seedlings. If these trends continue, AirBlock™ stock will grow to be larger than Styroblock™ stock, and thus this stock type shows promise.

Container type did not affect the overall extent to which ectomycorrhizal fungi colonized seedlings either in the nursery, or in the field after outplanting, although lingering effects of copper root pruning appeared to decrease colonization by specific fungi. Copper root pruning has been shown to significantly increase colonization of root systems by *Thelephora terrestris* on *Pinus contorta* (Hunt 1990) and *Pisolithus tinctorius* on *Pinus taeda* (Ruehle 1985). Conversely, copper concentrations less than those typically employed in root pruning (e.g. Ruehle 1985, approximately 50 g/L $CuCO_3$), has been shown to significantly inhibit growth of *Amanita muscaria* (Kong 1995), *Laccaria laccata*, *Thelephora terrestris*, and *Suillus variegatus* (Jones & Muehlchen 1994). Moreover, colonization rates of *Pisolithus tinctorius* (Oh & We 1996), *Scleroderma flavidum* (Jones & Hutchinson 1985), and *Suillus bovinus* (Yi & Shu

2001), has been shown to decrease as soil copper concentrations increase. Ectomycorrhizal fungi appear to differ in sensitivity to copper exposure (Leyval *et al.* 1997). This may be the reason that the richness of ectomycorrhizal morphotypes was significantly reduced in Copperblock™ seedlings, while colonization rates were not affected.

Ectomycorrhizal Fungal Inoculation

Inoculation of seedlings with ectomycorrhizal fungi in the nursery did not result in differences in seedling size at lifting. Results here are not surprising because, in the nursery, seedlings are supplied with nutrients and water in excess. Therefore, growth stimulation in the nursery is not necessarily expected (Stenström 1990; Villeneuve *et al.* 1991; Quoreshi & Timmer 2000). Moreover, even without fungal inoculation, lodgepole pine seedlings almost always become colonized with ectomycorrhizal fungi while in the nursery. This apparently also happened in this study, as I found no difference in ectomycorrhizal colonization rates between inoculated seedlings and non-inoculated seedlings at lifting. In spite of this, after two years of growth in the field, seedlings inoculated with *R. rubescens* were colonized less than either *H. longicaudum* inoculated seedlings or non-inoculated controls. Moreover, the decreased richness and increased evenness of the *H. longicaudum*-inoculated seedlings can be attributed to the increased relative abundance of five of the 21 morphotypes found at the Will Lake sites, as well as the number of *Hebeloma* spp. among the fungal community.

Outplanted seedlings gradually become colonized with fungi native to the site (Hagerman *et al.* 1999; Jones *et al.* 2002). This may explain the depressed colonization rates of the *R. rubescens* inoculated seedlings, as fungi native to the site gradually displace nursery fungi. However, decreased colonization levels of *R. rubescens*-inoculated seedlings, in conjunction with essentially no above- or below-ground growth response, suggests that results may be attributed to inoculation and not to ectomycorrhizal formation per se. Results here provide no evidence that inoculation with *R. rubescens* resulted in successful colonization, as *Rhizopogon*-like morphotypes only accounted for a very small proportion of those observed. It is difficult to explain this result because it implies that *R. rubescens* inhibited colonization of new roots by native fungi, without colonizing them itself. It is possible that *R. rubescens* caused some physiological change in the pine that suppressed colonization by the other fungi. Fungal inoculation effects are not necessarily a consequence of the formation of the ectomycorrhizal relationship (Normand *et al.* 1996; Grange *et al.* 1997).

Ectomycorrhizal fungi have been shown to stimulate rooting of micropropagated cuttings of arbuscular mycorrhizal *Prunus* species, which are unable to form ectomycorrhizas (Grange *et al.* 1997). Additionally, ectomycorrhizal fungal inoculation has also been shown to improve fascicular rooting of *Pinus sylvestris* by as much as 90% over controls (Niemi *et al.* 2000). Moreover, Karabaghli-Degron *et al.* (1998) report stimulated root elongation and shoot growth resulting from inoculation, in the absence ectomycorrhiza formation, with *Picea abies* seedlings. These results, as well as evidence here, suggest that in the absence of the symbiotic relationship, the ectomycorrhizal fungus is still able to readily affect the host, potentially through the amendment of the

rhizosphere. Ectomycorrhizal fungi release various compounds into the ectomycorrhizosphere such as IAA, gibberellins, cytyokinins, and ethylene (Scagel & Linderman 1998; Martin *et al.* 2001; Niemi *et al.* 2002). In addition to phytohormones, ectomycorrhizal fungi also release compounds such as phenols and indoles (Ditengou *et al.* 2000; Martin *et al.* 2001), as well as oligosaccharidic and proteinaceous elicitors (Salzer *et al.* 1996). Therefore it is possible that, although inoculation with *R. rubescens* appears not to have resulted in successful colonization, inoculation effects were still observed after two growth seasons.

After two years of growth in the field, there were no longer any differences in the number of emergent roots produced by inoculated and non-inoculated seedlings. Colonization of seedling roots with ectomycorrhizal fungi has the potential to affect seedling root system architecture (Niemi *et al.* 2002). Ectomycorrhizae promote the generation of lateral roots (Karabaghli-Degron *et al.* 1998), inhibit the formation and development of root hairs (Ditengou *et al.* 2000), as well as potentially promote dichotomous branching of root tips (Kaska *et al.* 1999). Although root growth and root system development of *Pinus* spp. are modified by the ectomycorrhizal relationship (Smith & Read 1997), the resultant ectomycorrhizal root morphology is dependent upon the host and the fungal partner (Martin *et al.* 2001). Therefore, after two years of growth at the Will Lake sites, during which time seedling root systems became colonized by native fungi, it is not surprising that seedlings exhibited similar root emergence patterns.

Many laboratory studies have reported differences in growth rates (Marx *et al.* 1988; Walker & Kane 1997) physiological parameters (Dosskey *et al.* 1991; Wu *et al.* 1999; Mason *et al.* 2000), and water relations (Boyle & Hellenbrand 1991) between

mycorrhizal and non-mycorrhizal seedlings. When seedlings are inoculated with specific ectomycorrhizal fungi in the nursery, significant growth responses may result, however, growth retardation may also occur (Browning & Whitney 1992; Berch & Roth 1993; Walker & Kane 1997; Parladé *et al.* 2001). However as previously stated, and as results here indicate, growth response in the nursery is not necessarily expected. Nursery effects, specifically growth stimulation due to inoculation, generally disappear with time after outplanting. Growth response in the field, however, is different, and is dependent upon the fungus and the site. I found no significant growth response with respect to inoculation, most likely due to seedling root systems being colonized by native fungal community members. However, enhanced growth effects can be enduring, specifically with the introduction of non-native tree species, on harsh sites, or when water deficits are common (Marx *et al.* 1988; LoBuglio & Wilcox 1988; Garbaye & Churin 1997).

Landing Rehabilitation

Growth in the nursery occurs under ideal conditions, and many factors have the potential to affect the physiology and morphology of commercially produced seedlings once planted out. Although certain factors can either be controlled or eliminated while in the nursery, the overriding factor responsible for plantation establishment success is the planting microsite environment (Balisky *et al.* 1995; Jones *et al.* 2002; Simard *et al.* 2003). Root morphology of outplanted conifer seedlings is extensively influenced by site conditions such as water availability, nutrients, and soil physical and chemical properties (Burdett *et al.* 1983; Burdett 1990; Balisky *et al.* 1995; Krasowski *et al.* 1996). This is

why site preparation is essential for plantation establishment and growth when conditions are less than optimal (Bedford & Sutton 2000). Landing construction, and subsequent usage generally results in a reduction in site productivity. Therefore limiting conditions must be alleviated in order to permit successful reforestation (Bulmer 1998). My results indicate that this can be done through incorporation of topsoil and burn-pile debris. Moreover, rehabilitation utilizing topsoil and burn-pile debris appears to have resulted in increased early growth over that of the adjacent cutblock. This may be because seedlings planted in the cutblock had to compete with pinegrass (*Calamagrostis rubescens*), while landings remained clear of competing vegetation through most of the study period. During the second season pioneer species such as great mullein (*Verbascum thapsus*), common dandelion (*Taraxacum officinale*), common plantain (*Plantago major*) and Canada thistle (*Cirsium arvense*) began to spread over the landings. This additional competition may explain why pine seedlings were the same size on the cutblock and fully rehabilitated halves of the landings after one growing season, but much larger on the landings than the cutblocks after the second growing season. Vegetative competition between pinegrass and plantation pine is known to result in reduced growth of lodgepole pine seedlings (Simard *et al.* 2003), and may be partially responsible for the difference in seedling size.

The combination of tilling soil and incorporation of organic amendments (burn-pile debris and topsoil) improved soil conditions to levels where early growth of lodgepole pine equalled or surpassed the adjacent cutblock. Other studies have found alleviation of soil compaction alone is sufficient to restore site productivity (Dykstra & Curran 2000; Williamson & Neilsen 2000), however if the forest floor and significant

portions of the upper soil horizons are displaced, compaction mitigation and organic amendment may be required (Plotnikoff *et al.* 2002). The lowest seedling growth rates took place on tilled plots, which had similar soil densities to those of the untreated portions of landings. Soil physical processes are influenced by soil porosity and the distribution of soil pore size; hence infiltration and the transport of soil air and soil water are adversely affected by soil compaction (Bulmer 1998). Additionally, soil physical properties, as a result of compaction, increase soil resistance to root growth, and may also adversely affect root growth via disruption of soil thermal properties. Moreover, nutrient pools, and nutrient cycling are depleted and degraded, through the removal of the forest floor and upper soil horizons (Prescott *et al.* 2000; Simard *et al.* 2003). Incorporation of burn-pile debris and topsoil tended to increase nutrient levels and soil temperature in plots, which corresponded with superior growth rates for seedlings. Consequently, results here illustrate, that for these medium- to coarse-textured soils, simple tillage or ripping of soils may not be sufficient to fully restore site productivity.

In this study, differences in seedling growth, with respect to different rooting environments, may also be attributed to the variation in soil rooting zone temperature as well as the number of days where the minimum daily temperature remained above 3.5°C. Both landing plots experienced higher soil temperatures than the cutblock during the summer months, presumably due to shading from vegetation and the insulation provided by the forest floor. However, landing plots receiving topsoil and burn-pile debris were also warmer in the spring and fall. Root growth and water uptake rates are both adversely affected by low soil temperature (Lopushinsky & Max 1990; Sutton 1991; Landhäusser *et al.* 2001; Peng & Dang 2003), with low root zone temperature considered to be the

limiting factor responsible for poor conifer plantation establishment and success in northern and central British Columbia (Balisky *et al.* 1995; Balisky & Burton 1997). Addition of top soil and burn-pile debris to landings resulted in an increased mean daily soil root zone temperature, as well as an increase in the number of days where the minimum daily temperature was above 3.5°C, over the adjacent cutblock, countering potential growth suppression due to low soil temperature in the spring and fall (Lopushinsky & Max 1990; Landhäusser *et al.* 2002).

Consistent with expectations, root systems of seedlings planted in the cutblock were colonized by ectomycorrhizal fungi to a greater extent than were seedlings planted on landings. Additionally, the ectomycorrhizal fungal community was richer and more diverse in the cutblock. The amount of available ectomycorrhizal fungal inoculum in the soil has the potential to influence root system colonization levels (Jones *et al.* 2003). Forest organic soil horizons are where the highest concentration of ectomycorrhizae, and thus the highest levels of potential inoculum, tend to be located (Fleming *et al.* 1984; Simard *et al.* 1997; Harvey *et al.* 1997). Landing construction, removal of the forest floor and displacement of mineral soil, therefore results in a decrease in habitat for many ectomycorrhizal fungi as well as a decline in potential sources of inoculum. Additionally, alteration of the chemical or physical properties of the soil can also potentially affect the ectomycorrhizal fungal community (Jones *et al.* 2003). Addition of burn-pile debris to landing plots may perhaps have reduced inoculum potential. Similar to the effects of fire, addition of burn-pile debris to landing plots resulted in an increase in certain nutrient levels and soil pH (Thomas & Wein 1990; Herr *et al.* 1994). Discounting the effects of the fire itself, results reported here are similar to those reported by both Visser (1995)

and Stendell *et al.* (1999), where the diversity of ectomycorrhizas was found to be significantly reduced on burned sites. However as the present results suggest, decreased ectomycorrhizal colonization, diversity, and richness, on landing plots, appears to be primarily a consequence of reduced inoculum potential when compared to the adjacent cutblock.

Summary

Rehabilitation of log landings and temporary roads is required for many forest sites in British Columbia; however, more information is needed regarding practical cost effective methods to return landings to productive forest using accessible materials found on site. Interior lodgepole pine (*Pinus controrta* var. *latifolia*) seedlings were grown in Styroblocks™, Copperblocks™, or AirBlocks™, and inoculated with *Rhizopogon rubescens*, *Hebeloma longicaudum*, or left as non-inoculated controls. Seedlings were planted into fully rehabilitated landings (burn-pile debris and topsoil incorporated), tilled landings, and unprepared portions of the adjacent cutblock. After two seasons of growth seedlings planted on fully rehabilitated landings were 60% larger, more vigorous, and exhibited 78% greater absolute growth and 27% greater relative growth rates, than seedlings planted in the adjacent cutblock. Seedlings planted in the cutblock exhibited higher ectomycorrhizal colonization rates, as well as greater ectomycorrhizal richness. Copperblock™ seedlings were larger at planting and continued to exhibit greater absolute growth (by 56% over Styroblock™ and AirBlock™ seedlings), while AirBlock™ seedlings exhibited the highest relative growth rates (18% over Styroblock™). Inoculation with ectomycorrhizal fungi did not affect growth of seedlings in the field. Results indicate that landing rehabilitation, through the incorporation of recovered topsoil and burn-pile debris via mechanical tillage, provides a suitable rooting environment for successful reforestation.

Literature Cited

Agerer, R. 1987-2000. Colour Atlas of Ectomycorrhizae. Einhorn-Verlag Eduard Dietenberger. Schwäbisch Gmüng, Germany,

Aldrete, A., Mexal, J.G., Phillips, R., and Vallotton, A.D. 2002. Copper coated polybags improve seedling morphology for two nursery-grown Mexican pine species. For. Ecol. Manage. 163: 197-204.

Arnold, M.A. and Struve, D.K. 1989. Growing green ash and red oak in $CuCO_3$-treated containers increases root regeneration and shoot growth following transplant. J. Amer. Soc. Hort. Sci. 114: 402-406.

Arnold, M.A. and Struve, D.K. 1993. Root distribution and mineral uptake of coarse-rooted trees grown in cupric hydroxide-treated containers. HortScience 28: 988-992.

Balisky, A.C. and Burton, P.J. 1997. Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in the interior British Columbia. New For. 14: 63-82.

Balisky, A.C., Salonius, P., Walli, C., and Brinkman, D. 1995. Seedling roots and forest floor: misplaced and neglected aspects of British Columbia's reforestation effort? For. Chron. 71: 59-65.

Bauhus, J. and Meiwes, K.J. 1994. Potential use of plant residue wastes in forests of northwestern Germany. For. Ecol. Manage. 66: 87-106.

Bedford, L. and Sutton, R.F. 2000. Site preparation for establishing lodgepole pine in the sub-boreal spruce zone of interior British Columbia: the Bednesti trial, 10-year results. For. Ecol. Manage. 126: 227-238.

Berch, S.M. and Roth, A.L. 1993. Ectomycorrhizae and growth of Douglas fir seedlings preinoculated with *Rhizopogon vinicolor* and outplanted on eastern Vancouver Island. Can. J. For. Res. 23: 1711-1715.

Blake, G.R. and Hartge, K.H. 1986. Bulk Density. *In* Methods of Soil Analysis. Part 1, Physical and Mineralogical Methods. 2nd ed. Soil Science Society of America, Madison, WI. pp. 363-375.

Boyle, C.D. and Hellenbrand, K.E. 1991. Assessment of the effect of mycorrhizal fungi on drought tolerance of conifer seedlings. Can. J. Bot. 69: 1764-1771.

Bradford, J.M. 1986. Penetrability. *In* Methods of Soils Analysis. Part 1, Physical and Mineralogical Methods. 2nd ed. Soil Science Society of America, Madison, WI. pp. 1188.

Bremner, J.M. 1996. Nitrogen-Total. *In* Methods of Soil Analyaia. Part 3, Chemical Methods. 3rd ed. Soil Science Society of America, American Society of Agronomy, Madison. WI. pp. 1085-1121.

Browning, M.H.R. and Whitney, R.D. 1992. Field performance of black spruce and jack pine inoculated with selected species of ectomycorrhizal fungi. Can. J. For. Res. 22: 1974-1982.

Bulmer, C. 2000. Reclamation of forest soils with excavator tillage and organic amendments. For. Ecol. Manage. 133: 157-163.

Bulmer, C.E. 1998. Forest soil rehabilitation in British Columbia: a problem analysis. B.C. Ministry of Forests. Land Management Handbook. Victoria, B.C. Rep. LMH-44.

Burdett, A.N. 1981. Box-pruning the roots of container-grown tree seedlings. *In* Proc. Canadian containerized tree seedling symposium. *Edited by* J.B. Scarratt, C. Glerum, and C.A. Plexman. Toronto, Ont., September 14–16, 1981. Environment Canada, Canadian Forestry Service, and Ontario Ministry of Natural Resources, pp. 203–206.

Burdett, A.N. 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. Can. J. For. Res. 20: 415-427.

Burdett, A.N., Coates, H., Eremko, R., and Martin, P.A.F. 1986. Toppling in British Columbia's lodgepole pine plantations: significance, cause and prevention. For. Chron. 62: 433-439.

Burdett, A.N., Simpson, D.G., and Thompson, C.F. 1983. Root development and plantation establishment success. Plant Soil 71: 103-110.

Carr, W.W. 1988. Nutritional and soil compaction aspects of establishing forest cover on winter landings in the Fort St. James area. Can. For. Serv. and B.C. Min. For. Victoria, B.C. Rep. FRR 047.

Clarke, C. and Winter, R. 1986. Lodgepole pine root form trial. Jack fire – Final Report. B.C. Ministry of Forests. Victoria, B.C. Rep. RNX 7901.

Clarke, C. and Winter, R. 1987. Chemical root prune trial, Kidd Creek. Final Report. B.C. Ministry of Forests. Victoria, B.C. Rep. Sx82205Q.

Conlin, T.S.S. and Van den Driessche, R. 1996. Short-term effects of soil compaction on growth of *Pinus contorta* seedlings. Can. J. For. Res. 26: 727-739.

Ditengou, F.A., Béguiristain, T., and Lapeyrie, F. 2000. Root hair elongation is inhibited by hypaphorine, the indole alkaloid from the ectomycorrhizal fungus Pisolithus tinctorius, and restored by indole-3-acetic acid. Planta 211: 722-728.

Dong, H. and Burdell, A.N. 1986. Chemical root pruning of Chinese pine seedlings raised in cupric sulfide impregnated containers. New For. 1: 67-73.

Dosskey, M.G., Boersma, L., and Linderman, R.G. 1991. Role for the photosynthate demand of ectomycorrhizas in the response of Douglas fir seedlings to drying soil. New Phytol. 117: 327-334.

Dunn, G.M., Huth, J.R., and Lewty, M.J. 1997. Coating nursery containers with copper carbonate improves root morphology of five native Australian tree species used in agroforestry systems. Agroforest. Syst. 37: 143-155.

Dykstra, P.R. and Curran, M.P. 2000. Tree growth on rehabilitated skid roads in southeast British Columbia. For. Ecol. Manage. 133: 145-156.

Fleming, L.V., Deacon, J.W., Last, F.T., and Donaldson, S.J. 1984. Influence of propagating soil on the mycorrhizal succession of birch seedlings transplanted to a field site. Trans. Br. Mycol. Soc. 82: 707-711.

Garbaye, J. and Churin, J.L. 1997. Growth stimulation of young oak plantations inoculated with the ectomycorrhizal fungi *Paxillus involutus* with special reference to summer drought. For. Ecol. Manage. 98: 221-228.

Gee, G.W. and Bauder, J.W. 1986. Particle-size analysis. *In* Methods of Soil Analysis. Part 1, Physical and Mineralogical Methods. 2nd ed. Soil Science Society of America, Madison, WI. pp. 383-411.

Gingras, B.M. and Richard, S. 1999. On the development of air-slit containers: nursery growth and seedling performance in comparative plantations. Direction de la Recherche Forestiere, Ministere des Ressources Naturelles. Sainte Foy, Quebec. Rep. No. 130.

Gingras, B.M., Richard, S., and Robert, N. 2002. Comparative performance after five years of large sized conifers and broadleaves grown in air-slit containers. Direction de la Recherche Forestiere, Ministere des Ressources Naturelles. Sainte Foy, Quebec. Rep. No. 141.

Gomez, A., Powers, R.F., Singer, M.J., and Horwath, W.R. 2002. Soil compaction effects on growth of young ponderosa pine following litter removal in California's Sierra Nevada. Soil Sci. Soc. Am. J. 66: 1334-1343.

Goodman, D.M., Durall, D.M., Trofymow, J.A., and Berch, S.M. 1996. A manual of concise descriptions of North American ectomycorrhizae. Describing ectomycorrhizae. Mycologue Publications. Sidney, B.C.

Grange, O., Bärtschi, H., and Gay, G. 1997. Effect of the ectomycorrhizal fungus *Hebeloma cylindrosporum* on in vitro rooting of the micropropogated cuttings of arbuscular mycorrhiza-forming *Prunus avium* and *Prunus cerasus*. Trees 12: 49-56.

Greacen, E.L. and Sands, R. 1980. Compaction of forest soils. A review. Aust. J. Soil Res. 18: 163-189.

Hagerman, S.H., Jones, M.D., Bradfield, G.E., and Sakakibara, S.M. 1999. Ectomycorrhizal colonization of *Picea engelmannii* × *Picea glauca* seedlings planted across cut blocks of different sizes. Can. J. For. Res. 29: 1856-1870.

Harvey, A.E., Page-Dumroese, D.S., Jurgensen, M.F., Graham, R.T., and Tonn, J.R. 1997. Site preparation alters soil distribution of roots and ectomycorrhizae on outplanted western pine and Douglas-fir. Plant Soil 188: 107-117.

Hendershot, W.H. and Duquette, M. 1986. A simple barium chloride method for determining cation exchange capacity and exchangeable cations. Soil Sci. Soc. Am. J. 50: 605-608.

Herr, D.G., Duchesne, L.C., Tellier, R., McAlpine, R.S., and Peterson, R.L. 1994. Effect of prescribed burning on the ectomycorrhizal infectivity of a forest soil. Int. J. Wildland Fire 4: 95-102.

Hunt, G.A. 1990. Effect of styroblock design and copper treatment on morphology of conifer seedlings. General Technical Report RM. U.S. Dept. Agri. For. Serv. Fort Collins, Colo. pp 218-222.

Hunt, R. 1982. Plant growth curves: the functional approach to plant growth analysis. Edward Arnold, London, England. 248p.

Ingleby, K., Mason, P.A., Last, F.T., and Fleming, L.V. 1990. Identification of Ectomycorrhizae. Her Majesty's Stationary Office, London, England.

Jansson, K. and Wästerlund, I. 1999. Effect of traffic by lightweight forest machinery on the growth of young *Picea abies* trees. Scand. J. For. Res. 14: 581-588.

Jones, D. and Muehlchen, A. 1994. Effects of the potentially toxic metals, aluminum, zinc and copper on ectomycorrhizal fungi. J. Environ. Sci. Health 29: 949-966.

Jones, M.D., Durall, D.M., and Cairney, W.G. 2003. Ectomycorrhizal fungal communities in young forests regenerating after clearcut logging. New Phytol. 157: 399-422.

Jones, M.D., Hagerman, S.M., and Gillespie, M. 2002. Ectomycorrhizal colonization and richness of previously colonized, containerized *Picea engelmannii* does not vary across clearcuts when planted in mechanically site-prepared mounds. Can. J. For. Res. 32: 1425-1433.

Jones, M.D. and Hutchinson, T.C. 1985. The effect of mycorrhizal infection on the response of *Betula papyrifera* to nickel and copper. New Phytol. 102: 429-442.

Jones, M.D., Kiiskila, S., and Flanagan, A. 2002. Field performance of pine stock types: Two-year results of a trial on interior lodgepole pine seedlings grown in Styroblocks™, Copperblocks™, or Airblocks™. B.C. J. Ecosys. Manage. 2: 59-70.

Kalra, Y.P. and Maynard, D.G. 1991. Methods manual for forest soil and plant analysis. Forestry Canada, Northwest Region, Northern Forestry Centre. Edmonton, AB. Rep. NOR-X-319.

Karabaghli-Degron, C., Sotta, B., Bonnet, M., Gay, G., and Tacon, F.L. 1998. The auxin transport inhibitor 2,3,5-triiodobenzoic acid (TIBA) inhibits the stimulation of in vitro lateral root formation and colonization of the tap-root cortex of Norway spruce (*Picea abies*) seedlings by the ectomycorrhizal fungus *Laccaria bicolor*. New Phytol. 140: 723-733.

Kaska, D.D., Myllylä, R., and Cooper, J.B. 1999. Auxin transport inhibitors act through ethylene to regulate dichotomous branching of lateral root meristems in pine. New Phytol. 142: 49-58.

Kong, F.X. 1995. Influence of copper, manganese and pH on the growth and several enzyme activities in mycorrhizal fungus *Aminita muscaria*. Chemoshpere 30: 199-207.

Kranabetter, J.M. and Bulmer, C.E. 1995. Composting trial using pulp fibre waste and municipal sewage sludge. B.C. Min. For. Research Branch, Prince George Forest Region. Prince George, B.C. Forest Science Report.

Kranabetter, J.M. and Osberg, M. 1995. Landing reclamation trials in the Prince George region. B.C. Min. For. Research Branch, Prince George Forest Region. Prince George, B.C. Forest Science Report.

Krasowski, M.J., Hawkins, C.D.B., Coates, H., and Ott, P.K. 1996. Static tests of lodgepole pine stability in the central interior of British Columbia. Can. J. For. Res. 26: 1463-1472.

Krebs, C.J. 1999. Ecological Methodology. 2nd ed. Addison-Welsey Educational Publishers, Menlo Park, CA. 620p.

Lamhamedi, M., Lambany, G., Margolis, H., Renaud, M., Veilleux, L., and Bernier, P.Y. 2001. Growth, physiology, and leachate losses in *Picea glauca* seedlings (1+0) grown in air-slit containers under different irrigation regimes. Can. J. For. Res. 31: 1968-1980.

Landhäusser, S.M., DesRochers, A., and Lieffers, V.J. 2001. A comparison of growth and physiology in *Picea glauca* and *Populus tremuloides* at different soil temperatures. Can. J. For. Res. 31: 1922-1929.

Landhäusser, S.M., Muhsin, T.M., and Zwiazek, J.J. 2002. The effect of ectomycorrhizae on water relations in aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) at low soil temperatures. Can. J. Bot. 80: 684-689.

Leyval, C., Turnau, K., and Haselwandter, K. 1997. Effect of heavy metal pollution on mycorrhizal colonization and function: physiological, ecological and applied aspects. Mycorrhiza 7: 139-153.

Lloyd, D., Angrove, K., Hope, G., and Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops forest region. Research Branch, B.C. Min. For. Victoria, B.C. Rep. LMH 23.

LoBuglio, K.F. and Wilcox, H.E. 1988. Growth and survival of ectomycorrhizal and ectendomycorrhizal seedlings of *Pinus resinosa* on iron tailings. Can. J. Bot. 66: 55-60.

Lopushinsky, W. and Max, T.A. 1990. Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. New For. 4: 107-124.

Luce, C.H. 1997. Effectiveness of road ripping in restoring infiltration capacity of forest roads. Restor. Ecol. 5: 265-270.

Martin, F., Duplessis, S., Ditengou, F., Largange, H., Vioblet, C., and Layprie, F. 2001. Developmental cross talking in the ectomycorrhizal symbiosis: signals and communication genes. New Phytol. 151: 145-154.

Marx, D.H., Cordell, C.E., and Clark, A.I. 1988. Eight-year performance of loblolly pine with *Pisolithus* ectomycorrhizae on a good-quality forest site. South. J. Appl. For. 12: 275-280.

Mason, E.G. 1985. Causes of juvenile instability of *Pinus radiata* in New Zealand. N. Z. J. For. Sci. 15: 263-280.

Mason, P.A., Ibrahim, K., Ingleby, K., Munro, R.C., and Wilson, J. 2000. Mycorrhizal development and growth of inoculated *Eucalyptus globulus* (Labill.) seedlings in wet and dry conditions in the glasshouse. For. Ecol. Manage. 128: 269-277.

McLean, E.O. 1982. Soil pH and lime requirement. *In* Methods of Soil Analysis. Part 2, Chemical and Microbiological Properties. American Society of Agronomy, Madison, WI. pp. 199-224.

McNabb, D.H. 1994. Tillage of compacted haul roads and landings in the boreal forests of Alberta. For. Ecol. Manage. 66: 179-194.

Miller, R.E., Scott, W., and Hazard, J.W. 1996. Soil compaction and conifer growth after yarding at three coastal Washington locations. Can. J. For. Res. 26: 225-236.

Nelson, D.W. and Sommers, L.E. 1982. Total carbon, organic carbon. and organic matter. *In* Methods of Soil Analysis. Part 2, Chemical and Microbiological Properties. American Society of Agronomy, Madison, WI. pp. 539-579.

Niemi, K., Salonen, M., Ernstsen, A., Heinonen, H., and Häggman, H. 2000. Application of ectomycorrhizal fungi in rooting of Scots pine fascicular shoots. Can. J. For. Res. 30: 1221-1230.

Niemi, K., Vuorinen, T., Ernstsen, A., and Häggman, H. 2002. Ectomycorrhizal fungi and exogenous auxins influence root and mycorrhiza formation of Scots pine hypocotyl cuttings in vitro. Tree Physiol. 22: 1231-1239.

Normand, L., Bärtschi, H., Debaud, J.C., and Gay, G. 1996. Rooting and acclimatization of micropropogated cuttings of *Pinus pinaster* and *Pinus sylvestris* are enhanced by the ectomycorrhizal fungus *Hebeloma cylindrosporum*. Physiol. Plant. 98: 759-766.

Oh, K.I. and We, K.M. 1996. Ectomycorrhizal development and growth of *Pinus thunbergii* seedlings inoculated with *Pisolithus tinctorius* (KJ-1) in copper treated soil. J. Korean For. Soc. 85: 329-339.

Parladé, J., Cohen, M., Doltra, J., Luque, J., and Pera, J. 2001. Continuous measurement of stem-diameter growth response of *Pinus pinea* seedlings mycorrhizal with *Rhizopogon roseolus* and submitted to two water regimes. Mycorrhiza 11: 129-136.

Peng, Y.Y. and Dang, Q.L. 2003. Effects of soil temperature on biomass production and allocation in seedlings of four boreal tree species. For. Ecol. Manage. 181: 1-9.

Plotnikoff, M.R., Bulmer, C.E., and Schmidt, M.G. 2002. Soil properties and tree growth on rehabilitated forest landing in the interior cedar hemlock biogeoclimatic zone: British Columbia. For. Ecol. Manage. 170: 199-215.

Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. 22: 119-154.

Prescott, C.E., Maynard, D.G., and Laiho, R. 2000. Humus in northern forests: friend or foe? For. Ecol. Manage. 133: 23-36.

Quoreshi, A.M. and Timmer, V.R. 2000. Early outplanting performance of nutrient-loaded containerized black spruce seedlings inoculated with *Laccaria bicolor*: a bioassay study. Can. J. For. Res. 30: 744-752.

Radwan, M.A. 1992. Effect of forest floor on growth and nutrition of Douglas-fir and western hemlock seedlings with and without fertilizer. Can. J. For. Res. 22: 1222-1229.

Reynolds, G. 1989. Climatic data summaries for the biogeoclimatic zones of British Columbia. Research Branch, B.C. Ministry of Forests. Victoria, B.C.

Ritchie, G.A. and Dunlap, J.R. 1980. Root growth potential: its development and expression in forest tree seedlings. N. Z. J. For. Sci. 10: 218-248.

Ruehle, J.L. 1985. The effect of cupric carbonate on root morphology of containerized mycorrhizal pine seedlings. Can. J. For. Res. 15: 586-592.

Salzer, P., Hebe, G., Reith, A., Zitterell-Haid, B., Stransky, H., Gaschler, K., and Hager, A. 1996. Rapid reactions of spruce cells to elicitors released from the ectomycorrhizal fungus *Hebeloma crustuliniforme*, and inactivation of these elicitors by extracellular spruce cell enzymes. Planta 198: 118-126.

Scagel, C.F. and Linderman, R.G. 1998. Influence of ectomycorrhizal fungal inoculation on growth and root IAA concentrations of transplanted conifers. Tree Phys. 18: 739-747.

Senyk, J.P. and Wass, E.F. 1999. Soil compaction resulting from ground-based forestry practices and the impact on conifer tree growth. *In* Proc. Impact of machine traffic on soil and regeneration. February 1999. Edmonton, Alberta. *Edited by* B. McMorland and S. Corradini. Forest Engineering Research Institute of Canada, Special Report No. SR-133. pp 43-64.

Simard, S.W., Jones, M.D., Durall, D.M., Hope, G.D., Stathers, R.J., Sorensen, N.S., and Ziomonick, B.J. 2003. Chemical and mechanical site preparation: effects on *Pinus contorta* growth, physiology, and micro-site quality on steep forest sites in British Columbia. Can. J. For. Res. 33: 1495-1515.

Simard, S.W., Perry, D.A., Smith, J.E., and Molina, R. 1997. Effects of soil trenching on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. New Phytol. 136: 327-340.

Simpson, D.G. 1990. Frost hardiness, root growth capacity, and field performance relationships in interior spruce, lodgepole pine, Douglas fir, and western hemlock seedlings. Can. J. For. Res. 20: 566-572.

Simpson, D.G. and Ritchie, G.A. 1997. Does RGP predict field performance? A debate. New For. 13: 253-277.

Simpson, D.G. and Vyse, A. 1995. Planting stock performance: site and RGP effects. For. Chron. 71: 739-742.

Smith, S. E. and Read, D. J. 1997. Mycorrhizal Symbiosis. 2nd Ed. Academic Press. San Diego, California. 605p.

Steel, R.G.D., Torrie, J.H., and Dickey, D.A. 1997b. Principles and Procedures of Statistics: a Biometrical Approach. 3rd ed. McGraw-Hill, New York, New York. 666p.

Stendell, E.R., Horton, T.R., and Bruns, T.D. 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. Mycol. Res. 103: 1353-1359.

Stenström, E. 1990. Variation in the field response of *Pinus sylvestris* to nursery inoculation with four different ectomycorrhizal fungi. Can. J. For. Res. 20: 1796-1803.

Sutton, R.F. 1991. Soil properties and root development in forest trees: A review. Forestry Canada. Sault Ste. Marie, Ont. Information Report O-X-413.

Tabachnick, B.G. and Fidell, L.S. 2001. Using Multivariate Statistics. 4th Ed. Allyn & Bacon, Needham Heights, MA. 966p.

Thomas, P.A. and Wein, R.W. 1990. Jack pine establishment on ash from wood and organic soil. Can. J. For. Res. 20: 1926-1932.

Villeneuve, N., Tacon, F.l., and Bouchard, D. 1991. Survival of inoculated *Laccaria bicolor* in competition with native ectomycorrhizal fungi and effects on the growth of outplanted Douglas-fir seedlings. Plant Soil 135: 95-107.

Visser, S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol. 129: 389-401.

Walker, R.F. and Kane, L.M. 1997. Containerized jeffrey pine growth and nutrient uptake response to mycorrhizal inoculation and controlled release fertilization. West. J. Appl. For. 12: 33-40.

Wenny, D.L. 1988. Growth of chemically root-pruned seedlings in the greenhouse and the field. *In* Proceedings combined meeting of the Western Forest Nursery Association, Vernon, B.C. August 8–11, 1988. *Edited by* T.D. Landis. U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experimental Station, Technical Report RM-167, pp. 32–37.

Williamson, J.R. and Neilsen, W.A. 2000. The influence of forest site on rate and extent of soil compaction and profile disturbance of skid trails during ground-based harvesting. Can. J. For. Res. 30: 1196-1205.

Winter, R. and S. Low. 1990. Manual and chemical root pruning of lodgepole pine PSB 211 stock. B.C. Ministry of Forests, Victoria, B.C. SX86125Q interim report. 32p.

Wu, B., Watanabe, I., Hayatsu, M., and Nioh, I. 1999. Effect of ectomycorrhizae on the growth and uptake and transport of ^{15}N-labelled compounds by *Pinus tabulaeformis* seedlings under water-stressed conditions. Biol. Fert. Soils 28: 136-138.

Yi, H. and Shu, T. 2001. Excessive Cu and Zn affecting on distribution of the metals and activities of glycolytic and nitrogen incorporating key enzymes in mycelia of ectomycorrhizal fungi *Suillus bovinus*. J. Environ. Sci. 13: 337-341.

Table 2-1: Morphology of seedlings outplanted at Will Lake.

Factors / Levels	colonization at lifting (%)		stem volume index at lifting (cm^3)		stem volume index 2000 (cm^3)		stem volume index 2001 (cm^3)		shoot dry mass 2001 (g)		root dry mass 2001 (g)		seedling dry mass 2001 (g)		seedling vigour 2001	
Rooting environment																
Full Rehab	*na*		*na*		2.98±0.35	*b*	21.98±4.61	*c*	15.89±3.14	*b*	6.41±1.19	*b*	22.31±3.48	*b*	2.28±0.16	*b*
Tilled	*na*		*na*		2.41±0.30	*a*	9.05±2.12	*a*	9.26±3.15	*a*	3.56±0.65	*a*	12.83±3.70	*a*	2.14±0.13	*a*
Cutblock	*na*		*na*		2.99±0.36	*b*	13.57±2.72	*b*	7.95±1.37	*a*	3.47±1.08	*a*	11.42±1.54	*a*	2.12±0.16	*a*
p					*<0.001*		*<0.001*		*<0.001*		*<0.001*		*<0.001*		*0.001*	
Container type																
Airblock™	42.2±5.2	*a*	0.94±0.16	*a*	1.99±0.25	*a*	11.93±3.02	*a*	9.79±2.31	*a*	3.55±0.78	*a*	13.33±2.65	*a*	2.17±0.15	*a*
Copperblock™	43.3±5.8	*a*	1.57±0.18	*b*	3.44±0.34	*c*	19.11±4.26	*b*	12.82±3.27	*a*	5.12±1.11	*b*	17.94±3.81	*a*	2.20±0.16	*a*
Styroblock™	55.8±6.7	*a*	1.27±0.13	*b*	2.87±0.35	*b*	12.18±2.59	*a*	11.44±3.26	*a*	5.26±1.34	*b*	16.70±4.10	*a*	2.15±0.15	*a*
p	*0.1*		*<0.001*		*<0.001*		*<0.001*		*0.4*		*0.04*		*0.1*		*0.5*	
Fungal inoculum																
H. longicaudum	46.7±5.7	*a*	1.26±0.19	*a*	2.86±0.35	*a*	15.08±3.27	*a*	11.21±2.57	*a*	4.60±1.09	*a*	15.80±3.15	*a*	2.14±0.16	*a*
R. rubescens	50.0±6.6	*a*	1.36±0.18	*a*	2.70±0.36	*a*	13.65±3.42	*a*	10.54±2.43	*a*	4.32±0.94	*a*	14.86±2.86	*a*	2.20±0.15	*a*
Control	44.7±5.7	*a*	1.16±0.17	*a*	2.75±0.32	*a*	14.77±3.71	*a*	11.57±3.63	*a*	4.62±1.32	*a*	16.19±4.41	*a*	2.19±0.16	*a*
p	*0.8*		*0.3*		*0.08*		*0.4*		*0.5*		*0.6*		*0.4*		*0.8*	
p root × cont	*na*		*na*		*0.03*		*<0.001*		*0.6*		*0.9*		*0.6*		*0.1*	
p root × inoc	*na*		*na*		*0.1*		*0.5*		*0.2*		*0.2*		*0.04*		*0.06*	
p cont × inoc	*<0.001*		*0.7*		*0.3*		*0.04*		*0.9*		*0.7*		*0.8*		*0.05*	

Note: Values shown are overall means per seedling level of each factor, and are shown ± 1SE (*na* indicates not applicable). Values followed by different letters, within the same column and factor; indicate a significant difference between means (Tukey's *W*, α=0.05, n=8, n=20 for stem volume index and seedling vigour).

Table 2-2: Root emergence patterns of seedlings outplanted at Will Lake.

Factors / Levels	Total Roots Per Seedling		Emergent root growth from root plug sections (percent of total new roots)					
			Top		Middle		Bottom	
Root Emergence at Lifting†								
Container Type								
AirBlock™	48.8± 7.9	*a*	19.2±4.0	*b*	30.7±3.9	*b*	52.7± 8.1	*a*
Copperblock™	72.5±16.9	*b*	12.8±2.8	*b*	23.0±4.0	*a*	70.3±22.9	*a*
Styroblock™	46.8± 9.3	*a*	7.1±2.0	*a*	15.6±4.6	*a*	76.7±23.7	*a*
p	*0.004*		*<0.001*		*<0.001*		*0.09*	
Fungal inoculum								
H. longicaudum	55.0± 9.6	*ab*	15.0±4.0	*a*	22.3±4.2	*a*	66.0±22.4	*a*
R. rubescens	42.8± 8.4	*a*	12.3±3.1	*a*	24.6±5.6	*a*	75.6±25.1	*a*
Control	70.3±16.6	*b*	12.1±3.4	*a*	23.0±4.6	*a*	62.3± 8.0	*a*
p	*0.005*		*0.8*		*0.3*		*0.3*	
p cont × inoc	*<0.001*		*0.2*		*0.7*		*0.3*	
Root emergence 2001‡								
Rooting Environment								
Full Rehab	53.7±6.7	*a*	10.7±2.7	*a*	20.1±4.0	*a*	69.1±4.8	*a*
Tilled	46.4±4.6	*a*	10.9±2.6	*a*	24.4±3.7	*a*	64.5±4.6	*a*
Cutblock	49.0±6.1	*a*	10.2±3.0	*a*	19.9±4.1	*a*	69.9±4.5	*a*
p	*0.2*		*0.9*		*0.09*		*0.1*	
Container Type								
Airblock™	47.4± 5.6	*a*	11.3±3.0	*a*	25.5±4.0	*a*	63.2±4.8	*a*
Copperblock™	51.8±10.7	*a*	10.9±2.5	*a*	19.9±4.2	*a*	69.2±4.6	*a*
Styroblock™	51.3± 7.1	*a*	9.5±2.6	*a*	17.3±3.2	*a*	73.3±3.7	*a*
p	*0.5*		*0.7*		*0.1*		*0.08*	
Fungal Inoculum								
H. longicaudum	50.5±6.6	*a*	10.4±3.0	*a*	23.0±3.9	*a*	66.7±4.3	*a*
R. rubescens	47.6±6.0	*a*	10.5±2.8	*a*	21.1±3.9	*a*	68.4±4.7	*a*
Control	51.9±9.6	*a*	10.9±2.4	*a*	21.0±4.2	*a*	68.2±5.0	*a*
p	*0.7*		*0.7*		*0.05*		*0.2*	
p cont × inoc	*0.4*		*0.05*		*0.6*		*0.1*	
p root × cont	*0.5*		*0.009*		*0.6*		*0.2*	
p root × inoc	*0.03*		*0.1*		*0.1*		*0.2*	

† Emergent root patterns at lifting derived from root growth capacity testing of a random sample of seedlings selected during lifting and subsequently analyzed in the lab (n=8).

‡ Root emergence 2001 represents random selection of seedlings harvested after the second season of field growth (n=8).

Note: Root plugs were divided into three equal sections, with the number of emergent roots greater than 1cm in length counted in each third. Total roots values represent the mean number of emergent roots per seedling, and are shown ± 1SE. Root plug section values represent the mean number of emergent roots as a proportion of the total number of emergent roots, and are shown ± 1SE. Mean values followed by different letters, within the same column and factor, indicate a significant difference between values (Tukey's *W*, α=0.05).

Table 2-3: Rooting zone soil physical properties for rehabilitated landings and adjacent cutblock plots at Will Lake.

Treatment	Bulk Density (kg/m^3)		Sand (%)		Silt (%)		Clay (%)	
Full Rehab	878±48	*a*	53.3±4.9	*a*	35.7±3.4	*b*	11.0±3.3	*b*
Cutblock	920±45	*a*	50.8±3.6	*ab*	42.1±3.8	*b*	7.1±1.8	*a*
Tilled	1167±67	*b*	59.3±5.0	*bc*	25.2±2.9	*a*	15.5±3.1	*b*
Control	1229±84	*b*	58.8±3.7	*c*	30.1±3.2	*a*	10.8±2.6	*a*
p	*<0.001*		*<0.001*		*<0.001*		*<0.001*	

Note: Values shown are overall estimated marginal means per treatment for rooting zone (soil depth 0-17 cm), and are shown ± 1 SE. Control represents the untreated 5 m wide control strip across the centre of landings, where seedlings were not planted. Mean values followed by different letters, within the same factor; indicate a significant difference between values (Tukey's *W*, α=0.05, n=15).

Table 2-4: Rooting zone soil chemical properties for rehabilitated landings and adjacent cutblock plots at Will Lake.

Treatment	CEC (Ba) (cmol(+)/kg)	pH (H_2O)	Total C (%)	Total N (%)	Min. N (ppm)
Full Rehab	28.2±1.3 *b*	6.8±0.1 *c*	4.9±1.0 *b*	0.15±0.01 *b*	20.9±2.5 *b*
Cutblock	19.0±1.2 *a*	5.8±0.1 *a*	2.6±0.4 *a*	0.11±0.01 *b*	29.9±4.9 *c*
Tilled	35.0±2.0 *c*	6.5±0.1 *b*	2.0±0.4 *a*	0.07±0.01 *a*	10.1±2.2 *a*
Control	32.9±1.3 *bc*	6.3±0.1 *b*	2.9±0.8 *a*	0.08±0.02 *a*	16.2±3.0 *ab*
p	*<0.001*	*<0.001*	*0.001*	*<0.001*	*<0.001*

	Avail. P (ppm)	Exch. Ca (cmol(+)/kg)	Exch. Mg (cmol(+)/kg)	Exch. K (cmol(+)/kg)
Full Rehab	74.5±6.1 *b*	17.5±0.7 *b*	9.5±0.9 *b*	0.84±0.05 *b*
Cutblock	46.3±4.9 *a*	12.3±0.8 *a*	5.9±0.7 *a*	0.51±0.08 *a*
Tilled	37.9±2.6 *a*	19.6±1.0 *b*	14.6±1.4 *d*	0.72±0.09 *ab*
Control	40.8±4.1 *a*	18.6±0.7 *b*	13.5±1.0 *c*	0.52±0.05 *a*
p	*<0.001*	*<0.001*	*<0.001*	*0.007*

Note: Values shown are overall estimated marginal means per treatment for rooting zone (depth 0-17 cm), and are shown ± 1 SE. Mean values followed by different letters, within the same factor; indicate a significant difference between values (Tukey's *W*, α=0.05, n=15).

Figure 2-1: Will Lake field trial study site location. Interior lodgepole pine (*Pinus contorta* var. *latifolia*) seedlings were planted into three replicate landings in the southern interior of British Columbia near Falkland, British Columbia (50°27.17 N, 119°38.33 W, 1244 m asl, IDF dk2 03).

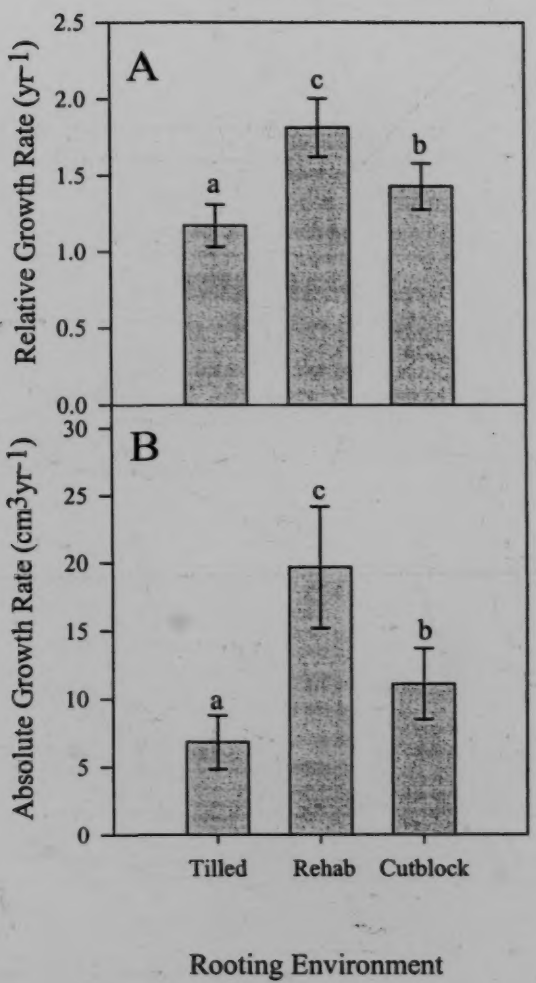


Figure 2-2: Growth rates of seedlings outplanted at Will Lake into tilled landings, rehabilitated landings, or the adjacent cutblock, following two seasons of growth in the field. Different letters associated with different bars indicate a significant difference within a category (Tukey's *W*, α=0.05), mean values are shown ± 1SE, n=20.

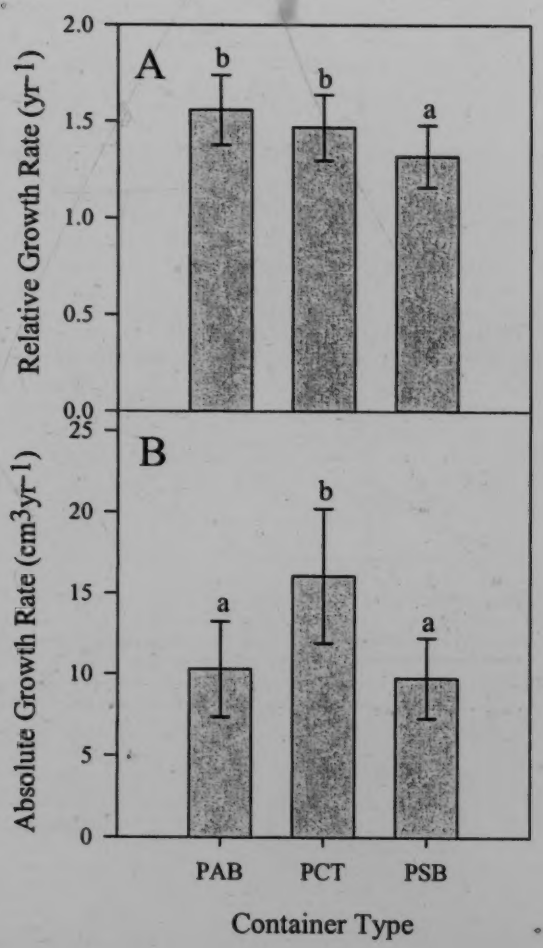


Figure 2-3: Growth rates of seedlings grown in AirBlocks™, Copperblocks™, or Styroblocks™, following two seasons of growth in the field at Will Lake. Different letters associated with different bars indicate a significant difference within a category (Tukey's *W*, α=0.05), mean values are shown ± 1SE, n=20 (AirBlock™ - PAB, Copperblock™ - PCT, Styroblock™ - PSB).

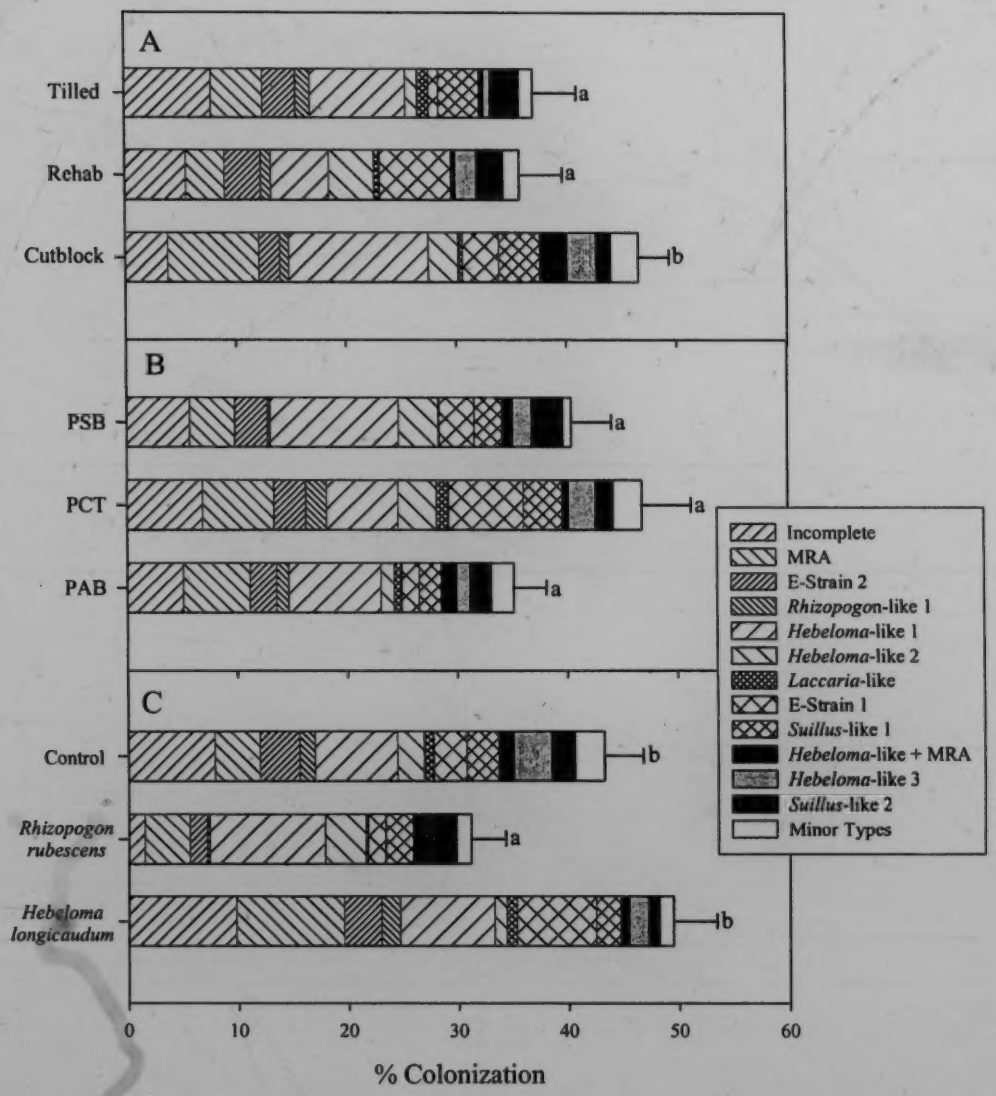


Figure 2-4: Relative abundance of the most common ectomycorrhizal morphotypes and overall percent colonization of root tips for seedlings planted at Will Lake, after two seasons of growth in the field. Morphological types found on less than 1% of root tips have been combined into minor types. Different letters associated with different bars indicate a significant difference between levels within a factor (Tukey's *W*, α=0.05), mean values are shown ± 1SE, n=8.

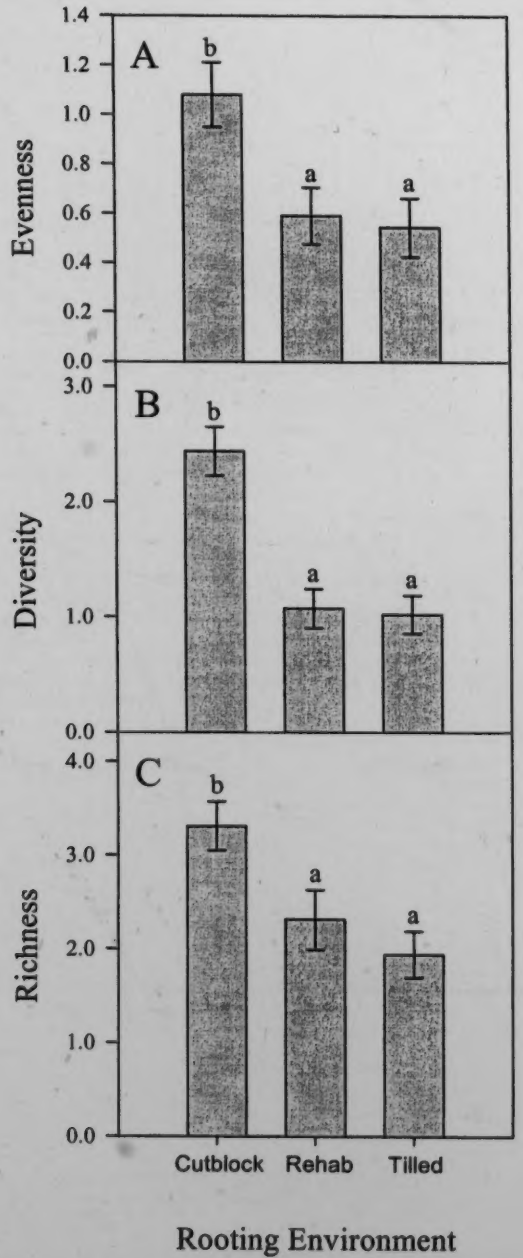


Figure 2-5: Ectomycorrhizal richness, diversity, and evenness, of seedling root tips after two seasons of growth in the field at Will Lake. Different letters associated with bars indicates a significant difference between values (Tukey's *W*, α=0.05). Bars represent overall mean values per seedling and are shown ± 1SE, n=8.

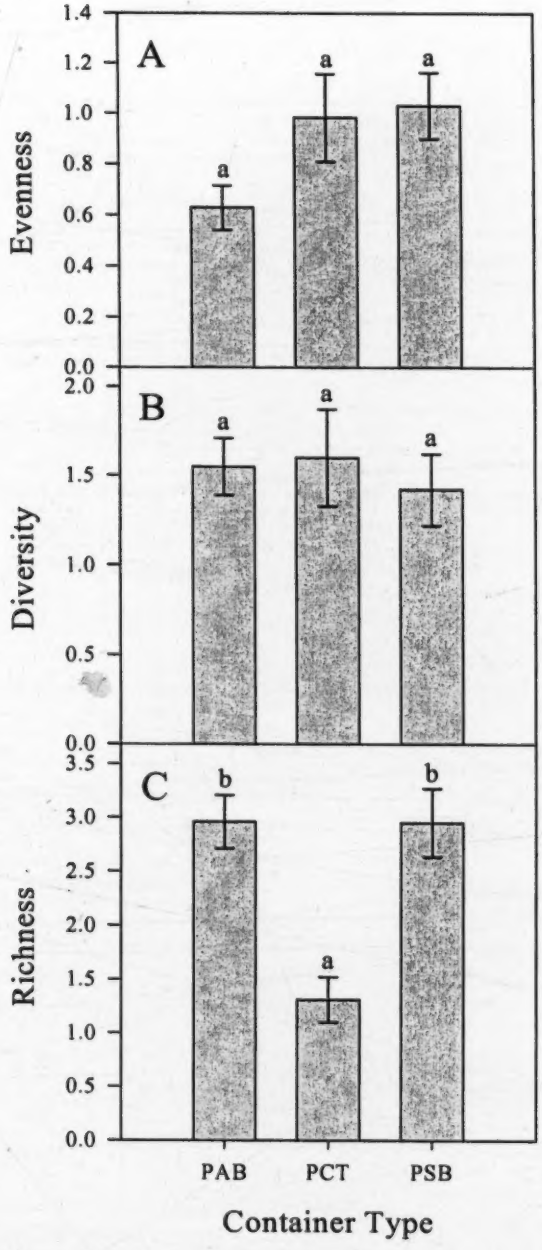


Figure 2-6: Ectomycorrhizal richness, diversity, and evenness, of seedling root tips after two seasons of growth in the field at Will Lake. Different letters associated with bars indicates a significant difference between values (Tukey's *W*, α=0.05). Bars represent overall mean values per seedling and are shown ± 1SE, n=8 (AirBlock™ - PAB, Copperblock™ - PCT, Styroblock™ - PSB).

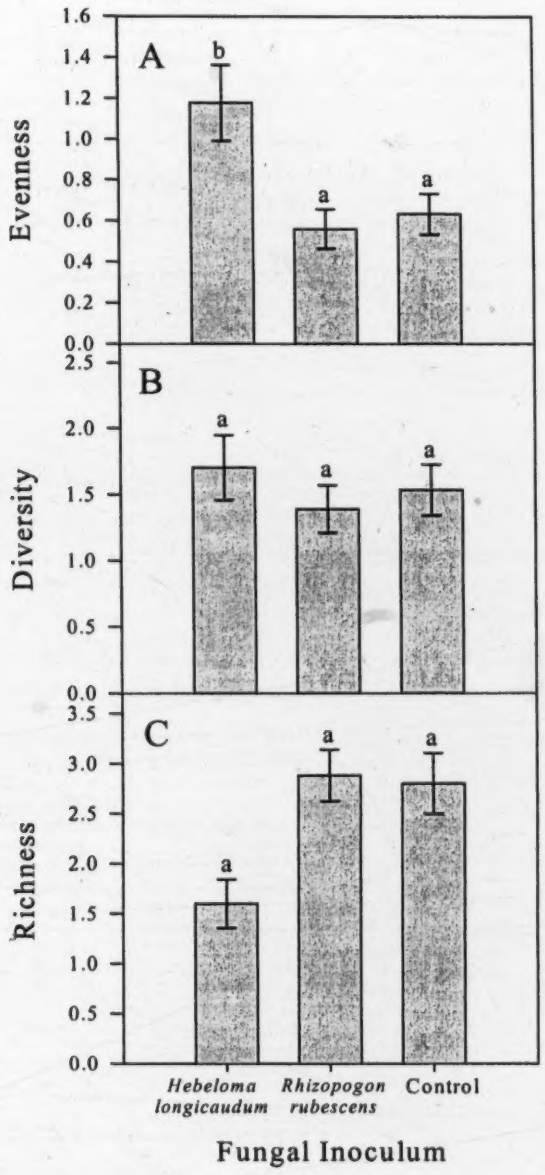


Figure 2-7: Ectomycorrhizal richness, diversity, and evenness, of seedling root tips after two seasons of growth in the field at Will Lake. Different letters associated with bars indicates a significant difference between values (Tukey's *W*, α=0.05). Bars represent overall mean values per seedling and are shown ± 1SE, n=8.

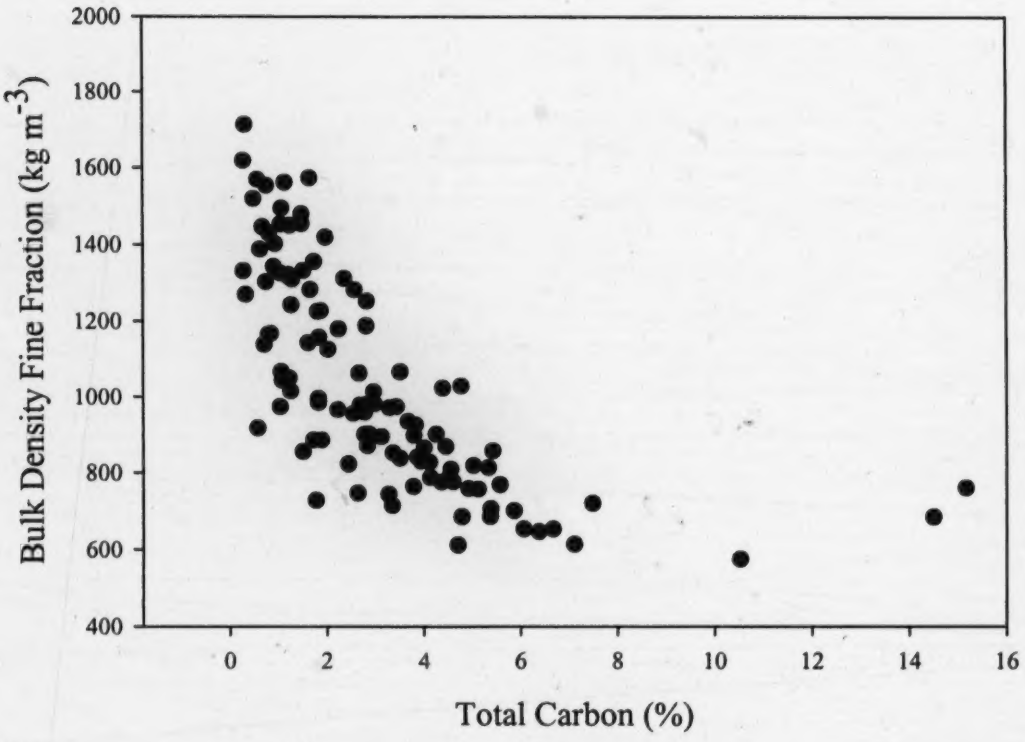


Figure 2-8: Relationship between the variation in soil bulk density and carbon concentration at Will Lake. Variation in soil properties was negatively correlated with carbon content ($p<0.001$, non-linear regression, $Y = -320.9 + 1843.9^{0.1697X} + 59.86X$, $R^2=0.67$).

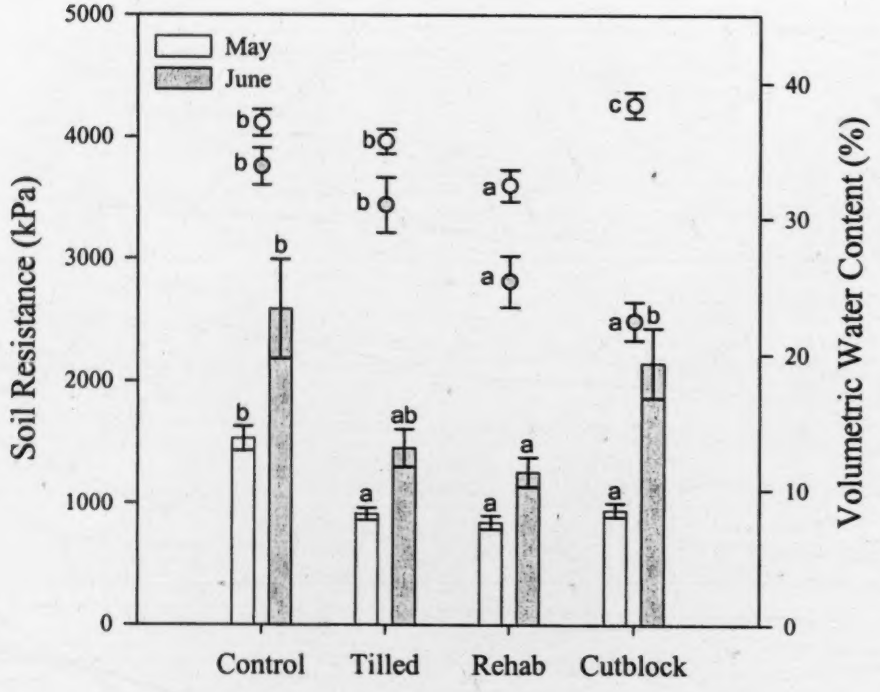


Figure 2-9: Soil resistance (bars) and water content (circles) during May and June 2002 at Will Lake. Soil resistance increased as soils dried from May to June. Different letters associated with bars and dots indicates a significant difference between values (Tukey's *W*, α=0.05). Mean values are shown ± 1 SE, n=10.

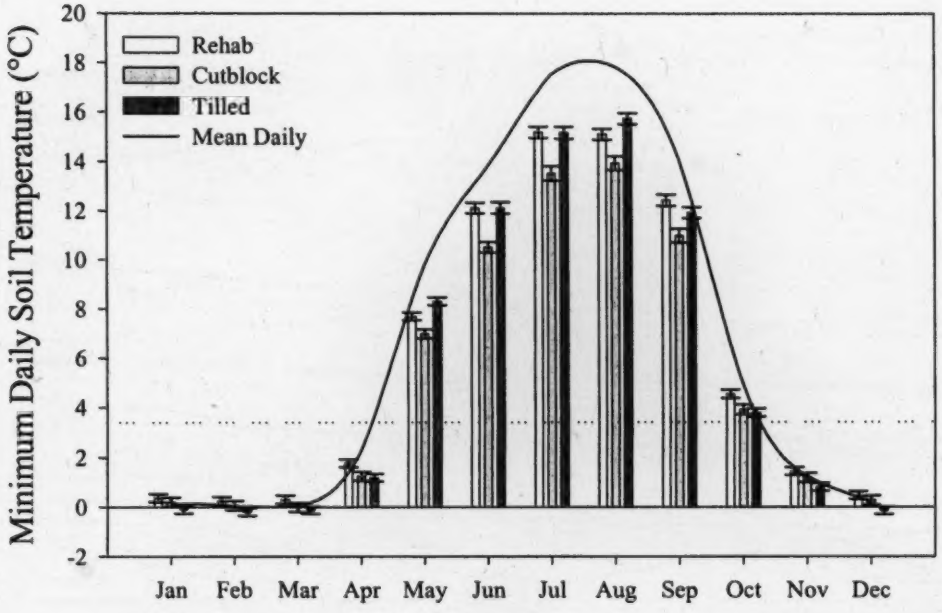


Figure 2-10: Minimum daily soil temperature at the bottom of the root plug (10-cm depth) for landings and the adjacent cutblock at Will Lake. Solid line represents the mean daily soil temperature at 10-cm depth. Dotted line indicates 3.5°C.Values presented are the mean minimum daily soil temperature per month, and are shown ± 1 SE.

Chapter 3

Forest floor planting of *Pinus contorta* var. *latifolia* seedlings in a high-elevation (ESSF) site in north-central British Columbia

Introduction

On many sites in British Columbia, it is customary to remove the organic soil horizons by mechanical or manual means in the locations where conifer seedlings will be planted. Site preparation that involves the removal of the surface organic horizons (screefing), has the potential to alter planting spots by increasing soil temperature (Delong *et al.* 1997), increasing available nutrients and water (Grossnickle & Heikurinen 1989; Radwan 1992), and decreasing competition from herbaceous species (Cain 1996; Simard *et al.* 2003). Planting seedlings directly in the undisturbed forest floor has been recently proposed in order to reduce costs and soil compaction associated with mechanical site preparation, and because mechanical site preparation may not be possible in adverse terrain (Heineman 1998). The forest floor has the potential to provide an ideal environment for seedling growth: it has low bulk density, good aeration, and readily available water and nutrients (Balisky *et al.* 1995).

In British Columbia, there are presently two container types commonly used for the commercial production of conifer seedlings (i.e. Styroblocks™ and Copperblocks™). A third type, AirBlocks™, account for only a small minority of commercial stock produced. The standard Styroblock™ container provides an economical means of

seedling propagation, but the tendency for new roots of Styroblock™-grown seedlings to grow primarily from the bottom of the root plug (Balisky *et al.* 1995) means that they emerge in lower soil horizons. Emergent root growth patterns and potential future stand instability (Mason 1985; Burdett *et al.* 1986) have lead to modifications of the standard Styroblock™-style container to allow for root pruning (Burdett *et al.* 1986). In Copperblocks™, root pruning is achieved through the addition of copper formulations to the interior walls and, in AirBlocks™ by slits in the container walls, resulting in a more diffuse, fibrous root system (Arnold & Struve 1993; Gingras & Richard 1999).

Conifer seedling root systems frequently become colonized with ectomycorrhizal fungi such as *Thelephora terrestris*, and *Wilcoxina mikolae* while growing in the nursery (Kropp & Langlois 1990). When inoculated with some strains of ectomycorrhizal fungi, seedlings can grow significantly more in the nursery than seedlings colonized with typical nursery fungi (Berch & Roth 1993; Walker & Kane 1997; Parladé *et al.* 2001). By contrast, inoculation with other strains can cause a suppression in growth rates (Bastide *et al.* 1995; Amitava *et al.* 2002). Very little is known about the potential interaction between ectomycorrhizal fungal inoculation and different container types. Ruehle (1985) concluded that the use of $CuCO_3$ (i.e. Copperblock™) had a negative (*Pinus strobus*), positive (*Pinus palustris*), or no effect (*Pinus taeda*), on ectomycorrhizal formation.

In the present study, I examined the effects of planting seedlings directly into the forest floor in contrast to manually screefed planting spots. I performed these comparisons for seedlings grown in Styroblocks™, Copperblocks™, or AirBlocks™, and for seedlings that had been inoculated or not with commercial ectomycorrhizal

fungal inocula. I hypothesized that lodgepole pine seedlings planted into manually screefed planting spots would exhibit improved growth and performance characteristics, when compared to seedlings planted directly into the forest floor. Additionally, based upon stock quality assessment prior to planting, I hypothesized that both Copperblock™ and AirBlock™ seedlings would exhibit similar root emergence patterns, with more new emergent roots produced from the upper portions of the root plug, when compared to Styroblock™ seedlings. Furthermore, if inoculation with specific ectomycorrhizal fungi in the nursery resulted in larger seedlings, I expected these differences to be maintained in the field.

Materials and Methods

Study Site

Interior lodgepole pine (*Pinus contorta* var. *latifolia*) seedlings were planted into a 156-hectare cutblock west of Hudson's Hope, British Columbia, Canada (56°19.17N, 122°30.41W, 1324 m asl, Figure 3-1). The cutblock was located in the Engelmann Spruce Subalpine Fir biogeoclimatic zone, Bullmoose moist very cold variant, site series 01 (ESSF mv2 01), of the British Columbia Biogeoclimatic Ecosystem Classification scheme (Pojar *et al.* 1987; Lloyd *et al.* 1990). Underlying mineral soil is a sandy loam with up to 50% coarse colluvial fragments, with an overlaying 2-6 cm mor humus layer. Located on the lee side of the northern Rocky Mountains, this site is classified as moist, with mean annual precipitation of 780 mm, and very cold, with a mean daily temperature

of -0.3°C (Reynolds 1989). Shrub and herbaceous vegetation in the cutblock consisted of white-flowered rhododendron (*Rhododendron albiflorum*), black huckleberry (*Vaccinium membranaceum*), and bunchberry (*Cornus canadensis*), with a majority of the ground covered by red-stemmed feathermoss (*Pleurozium schreberi*). This cutblock had been clearcut logged in the winter of 1999/2000 with 50% of the coarse woody debris (slash) retained on site.

Nursery Treatments

One-year-old (1+0) interior lodgepole pine seedlings (seedlot 39505) were produced at the Pacific Regeneration Technology (PRT) Red Rock Nursery, Prince George, British Columbia, Canada. Seedlings were grown in new Styroblocks™ (PSB 410, 80 ml, Beaver Plastics Ltd., Edmonton, Alberta, Canada), Copperblocks™ (PCT 410, 80 ml, Beaver Plastics Ltd.), or AirBlocks™ (PAB 410, 80 ml, BCC Silviculture Technology, Landskrona, Sweden). Randomly selected blocks of each stock type were inoculated with one of two fungal inocula: a spore slurry of *Rhizopogon rubescens* Tul. (Mycorrhizal Applications Inc., Grants Pass, Oregon, USA), or a mycelial slurry of *Hebeloma longicaudum* (Pers.: Fr.) Kummer (Mikro-Tek, Timmins, Ontario, Canada), or left as non-inoculated control seedlings. Ectomycorrhizal fungal inoculum was diluted seven fold with water, and applied with a watering can, as per supplier recommendations. Seedlings were inoculated once with *H. longicaudum* (June 1, 2000) and twice with *R. rubescens* (April 28 and June 19, 2000). Seedlings were grown to target morphological parameters: 14 cm for height and 2.5 mm for root collar diameter.

Seeds were sown in February 2000; seedlings were lifted on July 24, 2000, and planted on July 25, 2000.

During lifting, a random sample of seedlings from each combination of container type and fungal inoculation was selected for initial morphological measurement, ectomycorrhizal colonization, and assessment of potential root emergence. The height, root collar diameter, and ectomycorrhizal colonization were quantified on eight seedlings per nursery treatment. A random sample of 50 live root tips from the outer surface of each root plug was examined under a light microscope (70x and 400x). Root tips were classified as ectomycorrhizal if a mantle was present. To study seedling root emergence patterns, eight seedlings per nursery treatment were individually transplanted into 10×25 cm pots containing sand:peat:vermiculite (2:1:1 by volume) and grown for 10 days at 24°C with a 16 h photoperiod of 400 μmol m^{-2} s^{-1} PAR. Watering was to the point of runoff every three days. After harvest, the number of new emergent white roots, greater than 1 cm in length, was counted in three sections of the root plug (top one-third, middle one-third, bottom one-third).

Seedling Planting

Three 60×60 m sites, which were similar in slope and aspect, vegetative cover, and slash load, were selected within the cutblock. Each replicate site was divided randomly in half to accommodate the two different planting methods. Planting spots were either manually screefed (boot or planting shovel) to remove the overlaying forest floor and expose the mineral soil, or were left undisturbed with only coarse woody debris

removed from the planting spot. In the summer of 2000, 50 seedlings from each of the nine nursery treatments were planted, randomly interspersed at approximately 2 m spacing, in each half of the sites (2700 seedlings total). Regardless of planting method, planting sites were selected for optimal microsite conditions, as per operational planting procedures. For example, planting spots were generally located next to stumps, boulders, etc. to avoid seedling stem deformities resulting from movement within the heavy snow pack over the winter.

Soil samples were collected from randomly selected locations within each site (n=5) during seedling harvest. Soil samples were air-dried and coarse fragments (diameter >2 mm) within the sample were screened out. The sieved, air-dry soil samples were subsequently analyzed for total C and N, mineralizable N, soil pH, available P, CEC (cation exchange capacity), and exchangeable K at the British Columbia Ministry of Forests Research Branch Laboratory. Total soil C and N were determined by a dry combustion method (Nelson & Sommers 1982) using an automated Fisons NA-1500 analyzer. Mineralizable N was determined from ammonium-N in a KCl extract of soil following a two-week anaerobic incubation at 30°C (Bremner 1996). The soil pH was determined on a 1:2 (v/v) soil to distilled water slurry (McLean 1982). Available P was determined by extraction with ammonium fluoride and hydrochloric acid (Kalra & Maynard). Soil CEC and exchangeable K were determined by extraction with barium chloride (Hendershot & Duquette 1986). Results from the chemical analysis are reported on an oven-dry weight basis.

Soils at the Graham River study area were generally homogeneous, however there were some differences noted between sites (Table 3-1). Site 3 had the highest pH,

lowest total carbon, and lowest total nitrogen. Site 2 had a higher carbon content than the other locations. These factors may have contributed to variability amongst seedling growth or mycorrhizal colonization in the field; however, since there were not replicate plots at each site, I cannot evaluate this. Moreover, soil analysis results conform to the normal range of values expected for the study area location, slope, and aspect (Dr. Chuck E. Bulmer, Soil Restoration Ecologist, Forest Practices Research Section, B.C. Ministry of Forests; Personal Communication, 2003).

Growth in the Field

Seedling growth was assessed at the end of each of the first two growing seasons (September 2000 and 2001). Twenty seedlings of each of the 18 nursery treatment / planting method combinations (three container types × three inoculation treatments × two planting method), from each site, were randomly selected for measurement in 2000. The same seedlings were measured again in 2001. Seedling height and diameter were used to determine seedling stem volume index (V).

[1] $$V = d^2 h$$

Where d is the stem ground level diameter and h is the seedling height from ground level to the tip of the terminal bud. Seedling growth was determined by the calculation of absolute growth rates (G), or the incremental change in seedling volume between the second season and the first season (Hunt 1982).

[2] $$G_{1-2} = \frac{V_2 - V_1}{T_2 - T_1}$$

Where V is seedling volume (equation [1]) and T is the time interval (growth season). To ascertain seedling growth rates irrespective of the initial seedling volume (after the first years growth) or the final seedling volume (after the second years growth), seedling relative growth rates (R) were calculated (Hunt 1982).

[3] $$R_{1-2} = \frac{\log_e V_2 - \log_e V_1}{T_2 - T_1}$$

Where V is seedling volume (equation [1]) and T is the time interval (growth season). Seedlings were also assessed for vigour at the end of the second season (2001), with seedlings assigned a number, from 0 to 3, based upon their growth, form, and survival (0-dead; 1-poor appearance, chlorotic and stunted, not likely to survive, minimal growth; 2-average seedling, green and healthy, adequate growth and form; 3- robust large seedling, lush green and healthy, excellent growth and form).

After two seasons of growth in the field a random sample of eight seedlings from each container × fungal inoculation × planting method treatment was harvested to assess seedling growth parameters (shoot dry mass, root dry mass, seedling dry mass, root to shoot ratio, and root emergence patterns) and ectomycorrhizal status of roots. Root emergence pattern was determined by counting the number of roots greater than 1 cm in

length emerging from the top, middle, and bottom thirds of the root plug. Subsequent to root emergence assessment, root plugs were washed to remove all soil and debris, and air-dried. Root plugs and shoots were oven dried to a constant mass at 60°C, and weighed.

Mycorrhizal Status

Root plugs were soaked in water and the roots were gently cleaned free of soil and debris. All roots, including those in the root plugs, were cut into approximately 2-cm pieces. All root tips on randomly selected root pieces were examined, until 200 root tips per seedling had been categorized (minimum of 1200 root tips per container × inoculum × planting method treatment, per site: 21,600 root tips per site). Ectomycorrhizae were separated into morphological types (Appendix III) using the methods of Goodman *et al.* (1996) and compared to descriptions published in Agerer (1987-2000) and Ingleby *et al.* (1990). Characteristics such as root-tip branching patterns and colour, surface texture and lustre, were determined under a stereomicroscope (40x). The hyphal patterns of the inner and outer mantle layers, presence of surface features such as cystidia, presence or absence of extramatrical hyphae, extramatrical hyphal ornamentation, colour of extramatrical hyphae, were determined on whole root mounts or mantle peels under the light microscope (400x or 1000x). Mantle peels were made by gently separating fungal tissue from root tissue using fine forceps and a hypodermic needle. Both dead root tips and root tips that were not colonized by ectomycorrhizal fungi were characterized as

non-mycorrhizal. Root tips exhibiting early stages of fungal colonization (such as incomplete mantle formation) were classified as 'incomplete'.

The richness of ectomycorrhizae on seedling roots was expressed as the number of ectomycorrhizal morphotypes observed per seedling (Jones *et al.* 2002a). Simpson's reciprocal index of diversity ($1/D$) was used to determine the diversity of the ectomycorrhizal community present on seedling roots (Krebs 1999).

[4] $$\frac{1}{D} = \frac{1}{\sum p_i^2}$$

Where $1/D$ is Simpson's reciprocal index (varies from 1 to the number of morphotypes found in the sample), and p_i is the proportion of morphotype i in the community. Ectomycorrhizal community equitability was expressed as Simpson's measure of evenness (E), which follows from Simpson's measure of diversity (Krebs 1999).

[5] $$E_{1/D} = \frac{1/D}{s}$$

Where $1/D$ is Simpson's reciprocal index (equation [4]), and s is the number of ectomycorrhizal morphotypes in the sample. Simpson's indices of diversity and evenness were chosen because they are relatively unaffected by rare ectomycorrhizal morphotypes in the sample. The percentage of roots colonized was calculated as the total number of ectomycorrhizal root tips divided by the total number of root tips examined. Relative

abundance was calculated as the number of ectomycorrhizal root tips of each morphotype, as a proportion of the total number of live ectomycorrhizal root tips examined per seedling. Ectomycorrhizal richness was calculated as the total number of morphotypes, including those classified as incomplete. Percent colonization, richness, diversity, and evenness, were determined on an individual seedling basis.

Experimental Design and Data Analysis

All plant variables were analyzed with respect to each of the following factors in a completely randomized full factorial design: site, container type, fungal inoculum, and planting method. Due to the fact that 'site' was not a replicated variable, site effects will not be discussed further. Prior to statistical analysis, data were examined to ensure assumptions of a multivariate analysis of variance were met (Steel *et al.* 1997; Tabachnick & Fidell 2001). All plant data were analyzed using the general linear model multivariate analysis of variance (SPSS version 10.0, SPSS Inc. Chicago IL and SAS version 8.0, Cary, NC). Soil chemical analysis results were analyzed using a one-way analysis of variance, with site as the factor. Separation of significant mean values was based upon an honestly significant difference using Tukey's *W* procedure, or multiple comparison *t*-tests where appropriate, with the significance level interpreted as $p<0.05$. Multiple comparison *t*-tests were used to separate significant mean values for planting method effects, as Tukey's *W* is not appropriate for a factor with only two levels. The means presented are overall estimated marginal mean values.

Results

Initial Seedling Morphology

At the time of planting, fungal inoculation (p=0.03) but not container type (p=0.8) affected seedling volume (Table 3-2). Seedlings inoculated with *R. rubescens* produced the greatest stem volume index, 5% larger (although not significant) than *H. longicaudum* seedlings and 33% larger than non-inoculated seedlings. These differences in seedling stem volume index at the time of planting resulted from significant differences in seedling height (p=0.002) but not diameter (p=0.1), as seedlings inoculated with either ectomycorrhizal fungus were up to 17% or 2.5 cm taller than non-inoculated seedlings (Appendix II). Non-inoculated control seedlings became colonized by ectomycorrhizal fungi while in the nursery, with approximately 55% of the control seedlings root tips being colonized with ectomycorrhizal fungi (Table 3-2); therefore inoculum effects can be attributed to the ectomycorrhizal fungus that is present rather than to mycorrhizal colonization per se.

Root emergence patterns at lifting were affected by both container type and inoculum treatment. Although there were no significant differences in the total number of emergent roots after 10 days under ideal conditions, (Table 3-3), the distribution of roots throughout the root plug was affected. Copperblock™ and AirBlock™ seedlings both produced significantly more, over 20%, of their new emergent root growth in the top portion of the root plug, while Styroblock™ seedlings produced only 13% of their new roots in the top of the plug (p<0.001). Effects were reversed at the bottom of the

root plug. Inoculation with mycorrhizal fungi tended to shift root emergence slightly from the top of the plug to the bottom of the plug.

Growth in the Field

Planting methods did not affect seedling stem volume index at the end of the first growing season in the field (2000, p=0.3, Table 3-2); however, after the second season (2001) seedlings planted in screefed planting spots were on average 6% larger, than seedlings planted directly in the forest floor (p=0.009). Differences in seedling volume index reflected differences in the absolute and relative growth rates of seedlings. Seedlings planted in screefed spots exhibited a 7 % higher absolute growth rate (p=0.007) and a 6% greater relative growth rate (p=0.01) than seedlings planted in the forest floor (Figure 3-2A). There was no effect of planting method on seedling vigour or stem and root dry mass (Table 3-2).

Container type also influenced seedling growth rates in the field even though it had not done so in the nursery. The shoots of Copperblock™ seedlings were larger than both Styroblock™ and AirBlock™ seedlings after the first season but only larger than the AirBlock™ seedlings after the second season of growth (Table 3-2). At the end of the 2001-growing season, there was no difference in volume index between Copperblock™ and Styroblock™ grown seedlings, and both were approximately 13% lager than seedlings grown in AirBlocks™ (p<0.001). These differences were due to 9 % higher absolute growth rates in Copperblock™ and Styroblock™ seedlings, than AirBlock™ seedlings (p=0.006, Figure 3-2B). Although still smaller in size after two

years growth, AirBlock™ seedlings exhibited a 15% greater relative growth rate over Copperblock™ seedlings and a 9% greater relative growth rate over Styroblock™ seedlings during the second growing season ($p<0.001$, Figure 3-2B). There was no difference noted in seedling vigour after two years growth amongst seedlings grown in different container types ($p=0.4$, Table 3-2).

The increased volume index observed in inoculated seedlings at lifting, continued over two years of growth in the field (Table 3-2). After the second field season inoculated seedlings retained approximately 13% greater volumes than non-inoculated seedlings ($p<0.001$), but did not differ significantly in shoot or root dry mass. Seedlings inoculated with *H. longicaudum* exhibited higher absolute growth rates than non-inoculated seedlings ($p=0.001$, Figure 3-2C), with seedlings inoculated with *R. rubescens* having intermediate values. Inoculation of seedlings in the nursery with ectomycorrhizal fungi did not significantly affect seedling vigour ($p=0.4$, Table 3-2) or relative growth rates ($p=0.5$), in the field.

Root Emergence

Following two years of growth in the field, large differences were noted in root emergence patterns. Seedlings planted directly into the forest floor produced 11% more new emergent roots than seedlings planted into screefed planting spots ($p=0.006$, Table 3-3). Container type also affected root emergence. AirBlock™ seedlings produced 12% more new roots than did either Copperblock™ seedlings or Styroblock™ seedlings ($p=0.007$), even though they had the smallest shoots and tended to have the lowest

overall root weight (Table 3-2). Inoculum treatment did not influence the numbers of new roots produced (p=0.6, Appendix II). The proportion of new roots emerging from each section of the root plug was not significantly affected by planting method, container type or inoculum treatment.

Mycorrhizal Status

Seedlings planted directly into the forest floor became more colonized by ectomycorrhizal fungi (53 ± 2.6%) than did seedlings planted into screefed planting spots (45 ± 2.5 %; p= 0.01, Figure 3-3A). Differences in colonization also reflected differences in the relative abundance of the most common ectomycorrhizal morphotypes colonizing seedling root systems. Forest floor-planted seedlings were colonized significantly more by four of the eight most common morphotypes (*Cenococcum*-like, p=0.006; *Hebeloma*-like I, p=0.009; MRA, p=0.03; *Hebeloma*-like II, p=0.03; Figure 3-3A). Although seedlings planted in the forest floor were colonized more than seedlings planted in screefed spots, different planting methods resulted in a similar ectomycorrhizal community structure developing on seedling root systems. Seedlings were colonized by an average of 3.1 ± 0.24 distinct morphotypes per seedling, with no difference in ectomycorrhizal richness (p=0.6), diversity (p=0.9) or evenness (p=0.8) associated with planting method (Appendix II).

The container type significantly affected seedling colonization levels at lifting (p<0.001). At lifting, seedlings grown in AirBlocks™ and Styroblocks™ exhibited two-fold greater colonization rates compared with Copperblock™ seedlings (Table 3-2).

Container type continued to affect the ectomycorrhizal status of seedling root systems even after two years growth in the field (p=0.02, Figure 3-3B). Colonization of AirBlock™ seedlings was higher than Styroblock™ seedlings, with Copperblock™ seedlings intermediate. As colonization levels increased, so too did the relative abundance of the *Hebeloma*+MRA morphotype (p=0.02, Figure 3-3B). The *Amphinema*-like morphotype was not found on any AirBlock™ seedlings, however AirBlock™ root systems exhibited greater relative abundance of the *Hebeloma*+MRA morphotype. Other morphotypes were not affected by the container treatment. The richness (p= 0.01, Figure 3-4A) of ectomycorrhizal morphotypes on AirBlock™ and Copperblock™ root systems was higher than on Styroblock™ root systems. Similarly, AirBlock™ and Copperblock™ root systems exhibited greater ectomycorrhizal diversity (p=0.03, Appendix II); however, although a significant container type effect was observed, there was no significant difference found between mean values (Tukey's W). Following the same general trend, both AirBlock™ and Copperblock™ root systems exhibited less ectomycorrhizal evenness than did Styroblock™ root systems (p=0.01, Appendix II). Styroblock™ root systems, which had reduced ectomycorrhizal diversity, exhibited higher evenness (0.82 ± 0.06) than either AirBlock™ (0.73 ± 0.06) or Copperblock™ (0.73 ± 0.06) root systems. Inoculation with ectomycorrhizal fungi in the nursery did not affect percentage of roots colonized, after two growth seasons in the field (p=0.5, Appendix II). Furthermore, no difference was found between inoculation treatments with respect to the relative abundance of the most common ectomycorrhizal morphotypes (Appendix II), with the exception of the *Hebeloma*-like I morphotype (p=0.008, Appendix II). Seedlings inoculated with *H. longicaudum* exhibited greater relative

abundance of the *Hebeloma*-like I morphotype (13.3 ± 3.5%), than did seedlings inoculated with *R. rubescens* (6.2 ± 2.3%) or non-inoculated seedlings (3.5 ± 1.7%). This may have contributed to the low ectomycorrhizal richness (p=0.01, Figure 3-4B) and diversity (p = 0.03, Appendix II) exhibited by seedlings colonized with *H. longicaudum*. Fungal inoculation did not affect ectomycorrhizal evenness (p=0.1, Appendix II).

Discussion

Planting Methods

Lodgepole pine seedlings planted into screefed planting spots exhibited greater absolute growth and relative growth after two seasons in the field; although significant, the differences in growth rates where minor. Screefing tends to improve growth at sites with high vegetative competition, high soil moisture content, and sub-optimal soil temperature (Balisky & Burton 1997; Page-Dumroese *et al.* 1997; McKay & Mason 2001). Conversely, planting seedlings directly into the forest floor is recommended for sites with shallow soils, or sites with a high risk of frost heaving (Balisky *et al.* 1995; Heineman 1998; Sahlén & Goulet 2002). While some studies have described increased seedling growth in response to site preparation methods that remove the forest floor (e.g. Grossnickle & Heikurinen 1989; Gomez *et al.* 2002), others have found the opposite (e.g. Radwan 1992; Hallsby 1995). The Graham River study area is a northern cool and wet location; therefore, it was not surprising that seedlings planted into screefed planting spots exhibited greater growth rates. However, contrary to my hypothesis, seedlings

planted in screefed spots were only marginally larger than seedlings planted directly into the forest floor. This may be because the soil in the study area is a well-drained sandy loam, and because vegetative competition was minimal.

In this study, differences in seedling growth, with respect to planting method, may be attributed to variation in soil temperature. Availability of water and root growth are both adversely affected by low soil temperature (Landhäusser *et al.* 2001), with mineral soils in northern and the central interior of British Columbia being consistently below optimal temperatures (Balisky *et al.* 1995). Exposure of the mineral soil has the potential to increase soil temperature, thus countering growth suppression due to low soil temperatures (Lopushinsky & Max 1990; Landhäusser *et al.* 2002). Below optimal soil temperature may also have contributed to the failure of root growth capacity and root emergence patterns at lifting to predict root growth capacity and root emergence patterns in the field. Although root growth potential has been correlated with the field performance of *Pinus contorta* (Simpson 1990), assessment of the root growth potential of nursery stock can be affected considerably by the test conditions (Simpson & Ritchie 1997). Seedlings outplanted at the Graham River study site were exposed to conditions vastly different from those used in the lab to determine root emergence at lifting (e.g. available water, soil temperature).

Marginal differences in the above-ground growth response to the different planting methods may be attributed to the greater number of new roots produced by seedlings planted in the forest floor. A greater number of new emergent roots, combined with the fact that roots of the forest floor-planted seedlings were able to access the nutrient-rich boundary between the organic horizon and the upper mineral soil horizon,

may have attributed to the marginal differences in shoot growth. Naturally regenerated seedlings develop root systems principally horizontal in orientation (Balisky *et al.* 1995); these exploit the upper most layers of the mineral soil, with concentrations of roots often observed near the boundary layer of the mineral soil and the organic layer. The initial survival and growth of outplanted conifer seedlings is dependent upon the ability of the seedlings to readily produce new emergent roots, thereby enabling the seedlings to establish a continuum between the substrate and the root plug (Ritchie & Dunlap 1980). Consequently, the inability of the newly planted seedling to quickly establish a soil-root interface may lead to extended periods of low or stagnant growth (Girard *et al.* 1997).

The forest floor, the organic soil horizons, is where the highest concentration of ectomycorrhizae tend to be located (Harvey *et al.* 1997) and, thus, it tends to have high levels of ectomycorrhizal fungal inoculum (Fleming *et al.* 1984; Simard *et al.* 1997), provided seedlings are planted soon after timber harvest (Baar 1997; Swift *et al.* 2000; Simard *et al.* 2003). Forest floor-planted seedling root systems were colonized with ectomycorrhizal fungi to a greater extent than screef-planted seedlings. An extensive network of mycelial strands and hyphal mats was observed in the organic layers directly above the mineral soil throughout the Graham River site, suggesting that increased colonization may have arisen from fungal inoculum found in the organic layers.

Container Type

Container type did not affect seedling size at lifting, although it did affect the distribution of roots produced from root plugs. As expected, Copperblock™ and

AirBlock™ seedlings generally produced a greater proportion of new emergent roots from the upper portions of the root plug. This is consistent with the results of other studies that found chemical and air pruning tended to result in more fibrous, dispersed root systems (Gingras & Richard 1999; Gingras *et al.* 2002; Jones *et al.* 2002b). In such root systems, root tips are positioned along the entire outer surface of the root plug, and are therefore able to access the planting substrate in any direction from all locations on the root plug (Burdett 1990).

There is ample evidence that root pruning initially affects the root architecture of newly planted seedlings; however, it is still unclear whether initial modification of root systems by chemical or air pruning affects tree growth in the long term. In the experiment presented here, container type did produce noteworthy results after outplanting. Copperblock™ seedlings had the highest mean volume and the highest absolute growth rate after two seasons. By contrast, although smaller in size at the end of the experiment, AirBlock™ seedlings exhibited the greatest relative growth rates during the second growth season in the field. AirBlock™ seedlings produced more new emergent roots over the two years than did other stock types, indicating that increased root growth coincided with increased shoot growth. Increased shoot and root growth was also associated with the highest colonization by ectomycorrhizal fungi.

Ectomycorrhizal Fungal Inoculation

Significant increases in growth (Walker 1999), drought stress tolerance and water uptake (Mason *et al.* 2000), hydraulic conductance (Muhsin & Zwiazek 2002), and net

photosynthesis (Mason *et al.* 2000), have been described in mycorrhizal seedlings when compared with non-mycorrhizal seedlings. Results here also show that increased ectomycorrhizal colonization results in increased relative growth rates of seedlings. Differences in percent colonization may possibly be attributed to growth rates, as AirBlock™ seedling root systems were more heavily colonized, possibly because they grew more slowly. AirBlock™ seedlings exhibited the greatest relative growth, combined with the lowest mean root dry mass. Moreover, Copperblock™ and Styroblock™ seedlings exhibited superior absolute growth, combined with greater mean root dry mass. Root colonization is affected by the initiation of the mycorrhizal association, growth of the fungus, and host root growth (Smith *et al.* 1986; Bruce *et al.* 1994). Reduction in percent colonization could be attributed to fungal carbohydrate limitation, in addition to a reduction in the formation of new mycorrhizas. Thus reduced hyphal growth can be attributed to decreased carbohydrate acquisition from the host (Bruce *et al.* 1994). Larger Copperblock™ and Styroblock™ seedlings therefore exhibited greater absolute growth combined with lesser ectomycorrhizal colonization, possibly due to limitations in carbohydrates available for the fungus, due to increased growth of the host.

Inoculation of seedlings while growing in the nursery resulted in significant increases in the size of seedlings at the time of lifting. While growing in the nursery, conifer seedlings frequently become colonized by ectomycorrhizal fungi (Kropp & Langlois 1990). However, when inoculated with specific ectomycorrhizal fungi, seedlings can potentially grow considerably more in the nursery than seedlings colonized by typical nursery fungi (Berch & Roth 1993; Walker & Kane 1997; Parladé *et al.* 2001).

Inoculated seedlings were larger at lifting, and remained consistently larger over the first two seasons of growth in the field. Similar results have been reported for *Pseudotsuga menziesii*, *Pinus contorta*, *P. ponderosa*, and *P. pinea*, whereby fungal inoculation increased seedling growth after outplanting (Walker & Kane 1997; Scagel & Linderman 1998; Parladé *et al.* 2001). Once planted seedlings encounter a variety of site-related factors that have the potential to retard growth and increase seedling mortality. Although inoculated seedlings in this experiment generally exhibited greater absolute growth rates, there was no difference in the relative growth rates between inoculated or non-inoculated seedlings. Growth stimulation in the nursery, as a result of inoculation, does not always continue after seedlings are planted out in the field (Loopstra *et al.* 1988; Cram *et al.* 1999). This is possibly due to the fact that, if planted on a recently logged site, seedlings become colonized by members of the ectomycorrhizal fungal community that inhabit the site (Hagerman *et al.* 1999; Jones *et al.* 2002a). Inoculated fungi also tend to disappear from root systems over time due to competition from native fungi. In some cases, growth stimulation associated with inoculation lasts for many years, especially on inhospitable sites, under conditions of water deficit, or when tree species are introduced to sites where inoculum of compatible ectomycorrhizal fungi is low (LoBuglio & Wilcox 1988; Marx *et al.* 1988; Garbaye & Churin 1997).

After two growing seasons following planting there were a total of 13 ectomycorrhizal morphotypes present on the root systems of seedlings outplanted at the Graham River study site. Although no distinction was found between inoculation treatments with respect to colonization levels, seedlings inoculated with *H. longicaudum* exhibited significantly lower ectomycorrhizal richness, possibly due to increased relative

abundance of *Hebeloma*-like morphotypes. *R. rubescens*-inoculated and non-inoculated seedlings exhibited almost identical ectomycorrhizal richness, demonstrating similarity in colonization by native fungi regardless of fungal inoculation. The preponderance of *Hebeloma*-like ectomycorrhizas, suggests that inoculation with *H. longicaudum* was successful. *Rhizopogon*-like morphotypes were absent from the root systems of all inoculated seedling. Thus it appears that inoculation with this fungus was not successful. The differences in colonization success between the two fungi may be attributed to differences in their life history strategies (Jones *et al.* 2003). Conifer seedling root systems undergo ectomycorrhizal fungal succession (Gibson & Deacon 1990), beginning in the nursery, and continuing when seedlings are colonized by native fungal community members. *H. longicaudum* is characterized as an early succession fungi (Hutchison & Piché 1995), while *R. rubescens* is often a dominant late succession fungus (Molina & Trappe 1994). Early successional fungi are typically less dependent upon exogenous carbohydrate supplies, and have a broader host range, than are late succession fungi (Hutchison & Piché 1995). Moreover, later succession fungi are only able to colonize new roots, and thereby effectively compete against early succession fungi by means of hyphal extension from other mycorrhizal roots (Jones *et al.* 2003). Results here agree with those of Khasa *et al.* (2001), who report successful inoculation of *Pinus contorta* seedlings with an early succession ectomycorrhizal fungi (*Hebeloma longicaudum*), while inoculation with a late succession ectomycorrhizal fungi (*Rhizopogon vinicolor*), resulted in poor ectomycorrhiza development.

Although growth in the nursery is important, growth in the field after outplanting is paramount. Inoculation of lodgepole pine seedlings in the nursery, with commercially

available ectomycorrhiza, resulted in larger stock, exhibiting greater absolute growth over the first two years in the field. Although inoculated seedlings exhibited greater absolute growth, relative growth rates were no different from non-inoculated control seedlings, indicating differences may continue over the next few years. However the minor growth response observed may not justify the additional expense of seedling inoculation.

Summary

A two-year field trial was conducted to determine the ectomycorrhizal status and growth of 1+0 interior lodgepole pine (*Pinus contorta* var. *latifolia*) seedlings in response to several production and planting variables. Seedlings were grown in Styroblocks™, Copperblocks™, or AirBlocks™, and inoculated with *Rhizopogon rubescens*, *Hebeloma longicaudum*, or left as non-inoculated controls. Seedlings were planted into manually screefed planting spots or directly into the forest floor, in a high-elevation cutblock located in the Engelmann Spruce Subalpine Fir biogeoclimatic zone of north-central British Columbia. After two seasons of growth, seedlings that were planted into manually screefed planting spots exhibited 7% greater growth rates. Seedlings planted into the forest floor produced 11% more new emergent roots, with 12% more new roots from the top portion of the root plug. Additionally, seedlings that were planted directly into the forest floor, were colonized by ectomycorrhizal fungi to a greater extent (by 19%) than seedlings planted into screefed planting spots. AirBlock™ seedlings exhibited the greatest relative growth rates (by 14% over Copperblock™ and Styroblock™ seedlings), while Copperblock™ seedlings exhibited the greatest absolute growth rates (by 13% over AirBlock™ seedlings). Inoculation of seedlings with either ectomycorrhizal fungus resulted in a 14% increase in seedling volume in the nursery, with the size differences maintained over two seasons of growth in the field.

Literature Cited

Agerer, R. Colour Atlas of Ectomycorrhizae. 1987-2000. Einhorn-Verlag Eduard Dietenberger. Schwäbisch Gmüng, Germany.

Amitava, R., Bhadoria, P.B.S., Das, D.K., and Rakshit, A. 2002. An overview of mycorrhizal symbioses. J. Interacademicia 6: 570-581.

Arnold, M.A. and Struve, D.K. 1993. Root distribution and mineral uptake of coarse-rooted trees grown in cupric hydroxide-treated containers. HortScience 28: 988-992.

Baar, J. 1997. Ectomycorrhizal root growth in scots pine stands in response to manipulation of litter and humus layers. Mycorrhiza 7: 89-94.

Balisky, A.C. and Burton, P.J. 1997. Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in the interior British Columbia. New For. 14: 63-82.

Balisky, A.C., Salonius, P., Walli, C., and Brinkman, D. 1995. Seedling roots and forest floor: misplaced and neglected aspects of British Columbia's reforestation effort? For. Chron. 71: 59-65.

Berch, S.M. and Roth, A.L. 1993. Ectomycorrhizae and growth of Douglas fir seedlings preinoculated with *Rhizopogon vinicolor* and outplanted on eastern Vancouver Island. Can. J. For. Res. 23: 1711-1715.

Bremner, J.M. 1996. Nitrogen-Total. *In* Methods of Soil Analyaia. Part 3, Chemical Methods. 3rd Ed. *Edited by* D.L. Sparks. Soil Science Society of America, Book Series no. 5. Soil Science Society of America, American Society of Agronomy, Madison. WI. pp. 1085-1121.

Bruce, A., Smith, S.E., and Tester, M. 1994. The development of mycorrhizal infection in cucumber: effects of P supply on root growth, formation of entry points and growth of infection units. New Phytol. 127: 507-514.

Burdett, A.N. 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. Can. J. For. Res. 20: 415-427.

Burdett, A.N., Coates, H., Eremko, R., and Martin, P.A.F. 1986. Toppling in British Columbia's lodgepole pine plantations: significance, cause and prevention. For. Chron. 62: 433-439.

Cain, M.D. 1996. Woody and herbaceous competition effects on the growth of naturally regenerated loblolly pine and shortleaf pines through 11 years. New For. 14: 107-125.

Cram, M.M., Mexal, J.G., and Souter, R. 1999. Successful reforestation of South Carolina sandhills is not influenced by seedling inoculation with *Pisolithus tinctorius* in the nursery. South. J. Appl. For. 23: 46-51.

de la Bastide, P.Y., Kropp, B.R., and Piché, Y. 1995. Vegetative interactions among mycelia of *Laccaria bicolor* in pure culture and in symbiosis with *Pinus banksiana*. Can. J. Bot. 73: 1768-1779.

Delong, H.B., Lieffers, V.J., and Blenis, P.V. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. 27: 1452-1457.

Fleming, L.V., Deacon, J.W., Last, F.T., and Donaldson, S.J. 1984. Influence of propagating soil on the mycorrhizal succession of birch seedlings transplanted to a field site. Trans. Br. Mycol. Soc. 82: 707-711.

Garbaye, J. and Churin, J.L. 1997. Growth stimulation of young oak plantations inoculated with the ectomycorrhizal fungi *Paxillus involutus* with special reference to summer drought. For. Ecol. Manage. 98: 221-228.

Gibson, F. and Deacon, J.W. 1990. Establishment of ectomycorrhizas in aseptic culture: effects of glucose, nitrogen and phosphorus in relation to successions. Mycol. Res. 94: 166-172.

Gingras, B.M. and Richard, S. 1999. On the development of air-slit containers: nursery growth and seedling performance in comparative plantations. Direction de la Recherche Forestiere, Ministere des Ressources Naturelles. Sainte Foy, Quebec. Rep. No. 130.

Gingras, B.M., Richard, S., and Robert, N. 2002. Comparative performance after five years of large sized conifers and broadleaves grown in air-slit containers. Direction de la Recherche Forestiere, Ministere des Ressources Naturelles. Sainte Foy, Quebec. Rep. No. 141.

Girard, S., Clement, A., Cochard, H., Boulet-Gercourt, B., and Guehl, J. 1997. Effects of desiccation on post-planting stress in bare-root Corsican pine seedlings. Tree Physiol. 17: 429-435.

Gomez, G.A., Powers, R.F., Singer, M.J., and Horwath, W.R. 2002. N uptake and N status in ponderosa pine as affected by soil compaction and forest floor removal. Plant Soil 242: 263-275.

Goodman, D.M., Durall, D.M., Trofymow, J.A., and Berch, S.M. 1996. A manual of concise descriptions of North American ectomycorrhizae. Describing ectomycorrhizae. Mycologue Publications. Sidney, B.C.

Grossnickle, S.C. and Heikurinen, J. 1989. Site preparation: water relations and growth of newly planted jack pine and white spruce. New For. 3: 99-123.

Hagerman, S.H., Jones, M.D., Bradfield, G.E., and Sakakibara, S.M. 1999. Ectomycorrhizal colonization of *Picea engelmannii* × *Picea glauca* seedlings planted across cut blocks of different sizes. Can. J. For. Res. 29: 1856-1870.

Hallsby, G. 1995. Field performance of outplanted Norway spruce: effects of organic matter amendments and site preparation. Can. J. For. Res. 25: 1356-1367.

Harvey, A.E., Page-Dumroese, D.S., Jurgensen, M.F., Graham, R.T., and Tonn, J.R. 1997. Site preparation alters soil distribution of roots and ectomycorrhizae on outplanted western pine and Douglas-fir. Plant Soil 188: 107-117.

Heineman, J. 1998. Forest floor planting: a discussion of the issues as they relate to various site-limiting factors. BC Ministry of Forests, Forest Site Management Section. Victoria, B.C. Silviculture Note 16.

Hendershot, W.H. and Duquette, M. 1986. A simple barium chloride method for determining cation exchange capacity and exchangeable cations. Soil Sci. Soc. Am. J. 50: 605-608.

Hunt, R. 1982. Plant growth curves: the functional approach to plant growth analysis. Edward Arnold, London, England. 248p.

Hutchison, L.J. and Piché, Y. 1995. Effects of exogenous glucose on mycorrhizal colonization in vitro by early-stage and late stage ectomycorrhizal fungi. Can. J. Bot. 73: 898-904.

Ingleby, K., Mason, P.A., Last, F.T., and Fleming, L.V. 1990-2000. Identification of Ectomycorrhizae. Her Majesty's Stationary Office, London, England.

Jones, M.D., Durall, D.M., and Cairney, W.G. 2003. Ectomycorrhizal fungal communities in young forests regenerating after clearcut logging. New Phytol. 157: 399-422.

Jones, M.D., Hagerman, S.M., and Gillespie, M. 2002a. Ectomycorrhizal colonization and richness of previously colonized, containerized *Picea engelmannii* does not vary across clearcuts when planted in mechanically site-prepared mounds. Can. J. For. Res. 32: 1425-1433.

Jones, M.D., Kiiskila, S., and Flanagan, A. 2002b. Field performance of pine stock types: Two-year results of a trial on interior lodgepole pine seedlings grown in Styroblocks™, Copperblocks™, or Airblocks™. B.C. J. Ecosys. Manage. 2: 59-70.

Kalra, Y.P. and Maynard, D.G. Methods manual for forest soil and plant analysis. Forestry Canada, Northwest Region, Northern Forestry Centre. Edmonton, AB. Rep. NOR-X-319.

Khasa, P.D., Sigler, L., Chakravarty, P., Dancik, B.P., Erickson, L., and McCurdy, D. 2001. Effect of fertilization on growth and ectomycorrhizal development of container-grown and bare-root nursery conifer seedlings. New For. 22: 179-197.

Krebs, C.J. 1999. Ecological Methodology. 2nd ed. Addison-Welsey Educational Publishers, Menlo Park, CA. 620p.

Kropp, B.R. and Langlois, C.G. 1990. Ectomycorrhizae in reforestation. Can. J. For. Res. 20: 438-451.

Landhäusser, S.M., DesRochers, A., and Lieffers, V.J. 2001. A comparison of growth and physiology in *Picea glauca* and *Populus tremuloides* at different soil temperatures. Can. J. For. Res. 31: 1922-1929.

Landhäusser, S.M., Muhsin, T.M., and Zwiazek, J.J. 2002. The effect of ectomycorrhizae on water relations in aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) at low soil temperatures. Can. J. Bot. 80: 684-689.

Lloyd, D., Angrove, K., Hope, G., and Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops forest region. Research Branch, B.C. Min. For. Victoria, B.C. Rep. LMH 23.

LoBuglio, K.F. and Wilcox, H.E. 1988. Growth and survival of ectomycorrhizal and ectendomycorrhizal seedlings of *Pinus resinosa* on iron tailings. Can. J. Bot. 66: 55-60.

Loopstra, E.M., Shaw, C.G.I., and Sidle, R.C. 1988. Ectomycorrhizal inoculation fails to improve performance of sitka spruce seedlings on clearcuts in southeastern Alaska. West. J. Appl. For. 3: 110-112.

Lopushinsky, W. and Max, T.A. 1990. Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. New For. 4: 107-124.

Marx, D.H., Cordell, C.E., and Clark, A.I. 1988. Eight-year performance of loblolly pine with *Pisolithus* ectomycorrhizae on a good-quality forest site. South. J. Appl. For. 12: 275-280.

Mason, E.G. 1985. Causes of juvenile instability of *Pinus radiata* in New Zealand. N. Z. J. For. Sci. 15: 263-280.

Mason, P.A., Ibrahim, K., Ingleby, K., Munro, R.C., and Wilson, J. 2000. Mycorrhizal development and growth of inoculated *Eucalyptus globulus* (Labill.) seedlings in wet and dry conditions in the glasshouse. For. Ecol. Manage. 128: 269-277.

McKay, H.M. and Mason, E.G. 2001. Modelling the effects of nursery and site management on the early performance of *Picea sitchensis* (Bong.) Carr. New For. 22: 111-131.

McLean, E.O. 1982. Soil pH and lime requirement. *In* Methods of Soil Analysis. Part 2, Chemical and Microbiological Properties. *Edited by* A.L. Page, R.H. Miller, and D.R. Keeney. American Society of Agronomy, Madison, WI. pp. 199-224.

Molina, R. and Trappe, J.M. 1994. Biology of the ectomycorrhizal genus, *Rhizopogon* I. Host associations, host-specificity and pure culture synthesis. New Phytol. 126: 653-675.

Muhsin, T.M. and Zwiazek, J.J. 2002. Ectomycorrhizas increase apoplastic water transport and root hydraulic conductivity in *Ulmus americana* seedlings. New Phytol. 153: 153-158.

Nelson, D.W. and Sommers, L.E. 1982. Total carbon, organic carbon. and organic matter. *In* Methods of Soil Analysis. Part 2, Chemical and Microbiological Properties. *Edited by* A.L. Page, R.H. Miller, and D.R. Keeney. American Society of Agronomy, Madison, WI. pp. 539-579.

Page-Dumroese, D., Jurgensen, M.F., Harvey, A.E., Graham, R.T., and Tonn, J.R. 1997. Soil changes and tree seedling response associated with site preparation in northern Idaho. West. J. Appl. For. 12: 81-88.

Parladé, J., Cohen, M., Doltra, J., Luque, J., and Pera, J. 2001. Continuous measurement of stem-diameter growth response of *Pinus pinea* seedlings mycorrhizal with *Rhizopogon roseolus* and submitted to two water regimes. Mycorrhiza 11: 129-136.

Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. 22: 119-154.

Radwan, M.A. 1992. Effect of forest floor on growth and nutrition of Douglas-fir and western hemlock seedlings with and without fertilizer. Can. J. For. Res. 22: 1222-1229.

Reynolds, G. 1989. Climatic data summaries for the biogeoclimatic zones of British Columbia. Research Branch, B.C. Ministry of Forests. Victoria, B.C.

Ritchie, G.A. and Dunlap, J.R. 1980. Root growth potential: its development and expression in forest tree seedlings. N. Z. J. For. Sci. 10: 218-248.

Ruehle, J.L. 1985. The effect of cupric carbonate on root morphology of containerized mycorrhizal pine seedlings. Can. J. For. Res. 15: 586-592.

Sahlén, K. and Goulet, F. 2002. Reduction of frost heaving of Norway spruce and scots pine seedlings by planting in mounds or in humus. New For. 24: 175-182.

Scagel, C.F. and Linderman, R.G. 1998. Influence of ectomycorrhizal fungal inoculation on growth and root IAA concentrations of transplanted conifers. Tree Phys. 18: 739-747.

Simard, S.W., Jones, M.D., Durall, D.M., Hope, G.D., Stathers, R.J., Sorensen, N.S., and Ziomonick, B.J. 2003. Chemical and mechanical site preparation: effects on *Pinus contorta* growth, physiology, and micro-site quality on steep forest sites in British Columbia. Can. J. For. Res. 33: 1495-1515.

Simard, S.W., Perry, D.A., Smith, J.E., and Molina, R. 1997. Effects of soil trenching on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. New Phytol. 136: 327-340.

Simpson, D.G. 1990. Frost hardiness, root growth capacity, and field performance relationships in interior spruce, lodgepole pine, Douglas fir, and western hemlock seedlings. Can. J. For. Res. 20: 566-572.

Simpson, D.G. and Ritchie, G.A. 1997. Does RGP predict field performance? A debate. New For. 13: 253-277.

Smith, S.E., St. John, B.J., Smith, F.A., and Bromley, J.L. 1986. Effects of mycorrhizal infection on plant growth, nitrogen and phosphorus nutrition in glasshouse-grown *Allium cepa* L. New Phytol. 103: 359-373.

Steel, R.G.D., Torrie, J.H., and Dickey, D.A. 1997. Principles and Procedures of Statistics: a Biometrical Approach. 3rd ed. McGraw-Hill, New York, New York. 666p.

Swift, K., Jones, M., and Hagerman, S. 2000. An initial look at mycorrhizal fungi and inoculum potential in high elevation forests. B.C. J. Ecosys. Manage. 1: 1-6.

Tabachnick, B.G. and Fidell, L.S. 2001. Using Multivariate Statistics. 4th ed. Allyn & Bacon, Needham Heights, MA. 966p.

Walker, R.F. 1999. Reforestation of an eastern Sierra Nevada surface mine with containerized jeffrey pine: seedling growth and nutritional responses to controlled release fertilization and ectomycorrhizal inoculation. J. Sustain. For. 9: 127-147.

Walker, R.F. and Kane, L.M. 1997. Containerized jeffrey pine growth and nutrient uptake response to mycorrhizal inoculation and controlled release fertilization. West. J. Appl. For. 12: 33-40.

Table 3-1: Chemical properties of forest soils in the Graham River study area.

Soil Factors		Site 1	Site 2	Site 3	*p*
CEC (Ba)	cmol kg^{-1}	7.168±0.480a	7.130±0.567a	6.788±0.995a	*0.9*
Exchangeable K	cmol kg^{-1}	0.016±0.012a	0.106±0.022a	0.072±0.009a	*0.2*
Mineralizable N	ppm	11.140±0.499a	11.080±0.772a	9.300±1.594a	*0.4*
Available P	ppm	28.500±6.529a	20.120±8.520a	18.640±3.596a	*0.5*
pH/H_2O		4.224±0.076ab	4.036±0.017a	4.786±0.300b	*0.03*
Total C	%	1.702±0.065a	2.486±0.260b	1.570±0.207a	*0.01*
Total N	%	0.076±0.004a	0.092±0.010a	0.071±0.004a	*0.1*

Note: Mean values are shown ± 1SE, n=5. Associated *p* values represent significance of the dependent variable, one-way analysis of variance, α=0.05. Mean values followed by different letters, within the same category; indicate a significant difference between values (Tukey's *W*, α=0.05).

Table 3-2: Morphology of seedlings outplanted at the Graham River.

Factors/ Levels	colonization at lifting[†] (%)	stem volume index at lifting[†] (cm^3)	stem volume index 2000[‡] (cm^3)	stem volume index 2001[‡] (cm^3)	shoot dry mass 2001[†] (g)	root dry mass 2001[†] (g)	seedling vigour[‡] 2001
Planting Method							
Forest floor	na	*na*	1.46±0.13a	4.85±0.48a	3.68±0.50a	1.50±0.30a	1.7±0.12a
Screefed	*na*	*na*	1.50±0.14a	5.14±0.51b	3.81±0.50a	1.48±0.22a	1.7±0.12a
p	*na*	*na*	*0.3*	*0.009*	*0.5*	*0.6*	*0.1*
Container Type							
AirBlock™	72.2±4.5b	1.46±0.12a	1.23±0.13a	4.53±0.46a	3.63±0.48a	1.35±0.25a	1.7±0.12a
Copperblock™	31.4±4.0a	1.44±0.12a	1.68±0.14c	5.39±0.53b	3.90±0.51b	1.55±0.25a	1.7±0.11a
Styroblock™	76.1±5.1b	1.37±0.10a	1.53±0.13b	5.07±0.49b	3.97±0.49b	1.56±0.30a	1.7±0.12a
p	*<0.001*	*0.8*	*<0.001*	*<0.001*	*0.001*	*0.03*	*0.4*
Fungal Inoculum							
H. longicaudum	61.9±6.2a	1.50±0.11b	1.57±0.14b	5.32±0.54b	3.89±0.50a	1.53±0.27a	1.7±0.11a
R. rubescens	60.9±5.2a	1.58±0.13b	1.51±0.13b	5.06±0.47b	3.85±0.51a	1.48±0.24a	1.7±0.12a
Control	55.8±6.2a	1.19±0.09a	1.36±0.13a	4.61±0.47a	3.52±0.48a	1.45±0.29a	1.6±0.13a
p	*0.6*	*0.03*	*<0.001*	*<0.001*	*0.06*	*0.7*	*0.4*
p plant×cont	*na*	*na*	*0.2*	*0.9*	*0.5*	*0.2*	*0.5*
p plant×inoc	*na*	*na*	*0.9*	*0.6*	*0.3*	*0.07*	*0.8*
p cont×inoc	*0.5*	*0.3*	*0.2*	*0.2*	*0.4*	*0.7*	*0.5*

Note: Values shown are overall means per seedling level of each factor, and are shown ± 1SE (*na* indicates not applicable). Values followed by different letters, within the same column and factor; indicate a significant difference between means (multiple comparison *t*-tests for planting method and Tukey's *W*, α=0.05). Seedling Characteristics: [†] n=8, [‡] n=20.

Table 3-3: Root emergence patterns of seedlings outplanted at the Graham River.

Factors / Levels	Total Roots Per Seedling	Number of emergent roots per root plug section (Number of roots as proportion of total new roots)					
		Top		Middle		Bottom	
Root emergence at lifting †							
Container type							
AirBlock™	77.3±4.8a	16.1±1.8ab	(20.1±1.4b)	20.8±1.4a	(27.4±1.3a)	40.4±2.8a	(52.5±2.0a)
Copperblock™	75.6±6.2a	17.6±1.9b	(23.4±1.1b)	19.2±1.7a	(26.1±1.4a)	38.9±3.8a	(50.6±2.0a)
Styroblock ™	90.0±7.1a	11.8±1.6a	(13.2±1.3a)	24.6±2.6a	(26.8±1.9a)	53.7±4.7b	(60.0±2.5b)
p	*0.2*	*0.047*	*(<0.001)*	*0.1*	*(0.8)*	*0.009*	*(0.003)*
Fungal inoculum							
H. longicaudum	85.3±6.3a	14.0±1.4a	(17.2±1.4a)	23.9±1.9a	(29.0±1.5b)	47.4±4.8a	(53.8±2.0ab)
R. rubescens	75.5±4.6a	13.8±1.8a	(17.8±1.8ab)	18.2±1.7a	(23.6±1.5a)	43.5±2.8a	(58.7±2.5b)
Control	82.1±1.5a	17.7±2.2a	(21.8±1.5b)	22.4±2.3a	(27.7±1.1ab)	42.0±4.3a	(50.5±2.1a)
p	*0.5*	*0.2*	*(0.03)*	*0.09*	*(0.02)*	*0.6*	*(0.02)*
p cont × inoc	*0.02*	*0.05*	*(0.1)*	*0.1*	*(0.02)*	*0.008*	*(0.02)*
Root emergence 2001 ‡							
Planting Method							
Forest Floor	30.2±3.8b	6.4±1.1a	(22.1±3.2a)	8.9±1.5a	(30.0±3.9a)	14.9±2.7a	(47.9±4.8a)
Screefed	27.4±3.7a	5.7±1.0a	(21.8±3.3a)	8.3±1.4a	(31.5±3.6a)	13.3±2.6a	(46.7±4.6a)
P	*0.006*	*0.08*	*(0.8)*	*0.1*	*(0.09)*	*0.02*	*(0.1)*
Container Type							
AirBlock™	31.1±3.5b	6.4±1.1a	(21.1±3.1a)	9.3±1.4a	(30.4±3.5a)	15.4±2.5b	(48.5±4.3a)
Copperblock™	27.5±3.8a	6.0±1.0a	(22.9±3.3a)	8.5±1.4ab	(31.5±3.6a)	13.1±2.6a	(45.7±4.4a)
Styroblock™	27.8±4.0a	5.7±1.1a	(21.8±3.3a)	8.1±1.5a	(30.4±4.2a)	14.0±2.9ab	(47.8±5.3a)
p	*0.007*	*0.1*	*(0.2)*	*0.04*	*(0.5)*	*0.04*	*(0.1)*
Fungal Inoculum							
H. longicaudum	28.4±3.6a	6.1±0.9a	(22.5±3.2a)	8.1±1.3a	(29.5±4.0a)	14.2±2.6a	(48.0±5.1a)
R. rubescens	29.5±3.8a	6.2±1.1a	(21.3±2.9a)	9.2±1.5a	(32.2±3.7a)	14.1±2.7a	(46.5±4.4a)
Control	28.6±4.2a	5.9±1.2a	(21.9±3.6a)	8.6±1.5a	(30.7±3.6a)	14.1±2.9a	(47.4±4.5a)
p	*0.6*	*0.9*	*(0.4)*	*0.1*	*(0.3)*	*0.8*	*(0.8)*
p cont × inoc	*0.3*	*0.9*	*(0.3)*	*0.01*	*(0.2)*	*0.9*	*(0.6)*
p cont × plant	*0.9*	*0.2*	*(0.2)*	*0.1*	*(0.1)*	*0.4*	*(0.02)*
p inoc × plant	*0.1*	*0.1*	*(0.5)*	*0.4*	*(0.8)*	*0.4*	*(0.7)*

† Emergent root patterns at lifting derived from root growth capacity testing, random sample of seedlings selected during lifting and subsequently analyzed in the lab (n=8).
‡ Root emergence 2001 represents random selection of seedlings harvested after the second season of growth (n=8).
Note: Root plugs were divided into three equal sections, with the number of emergent roots greater than 1cm in length counted in each third. Values shown represent the mean number of emergent roots, per seedling, and are shown ± 1SE. Values shown in parentheses represent the mean number of emergent roots per seedling, as a proportion of the total number of emergent roots, and are shown ± 1SE. Mean values followed by different letters, within the same column and factor; indicate a significant difference (multiple comparison *t*-tests for planting method and Tukey's *W*, α=0.05).

Figure 3-1: Graham River field trial study site location. Interior lodgepole pine (*Pinus contorta* var. *latifolia*) seedlings were planted into three replicate sites in a cutblock located west of Hudson's Hope, British Columbia (56°19.17 N, 122°30.41 W, 1324 m asl, ESSF mv2 01).

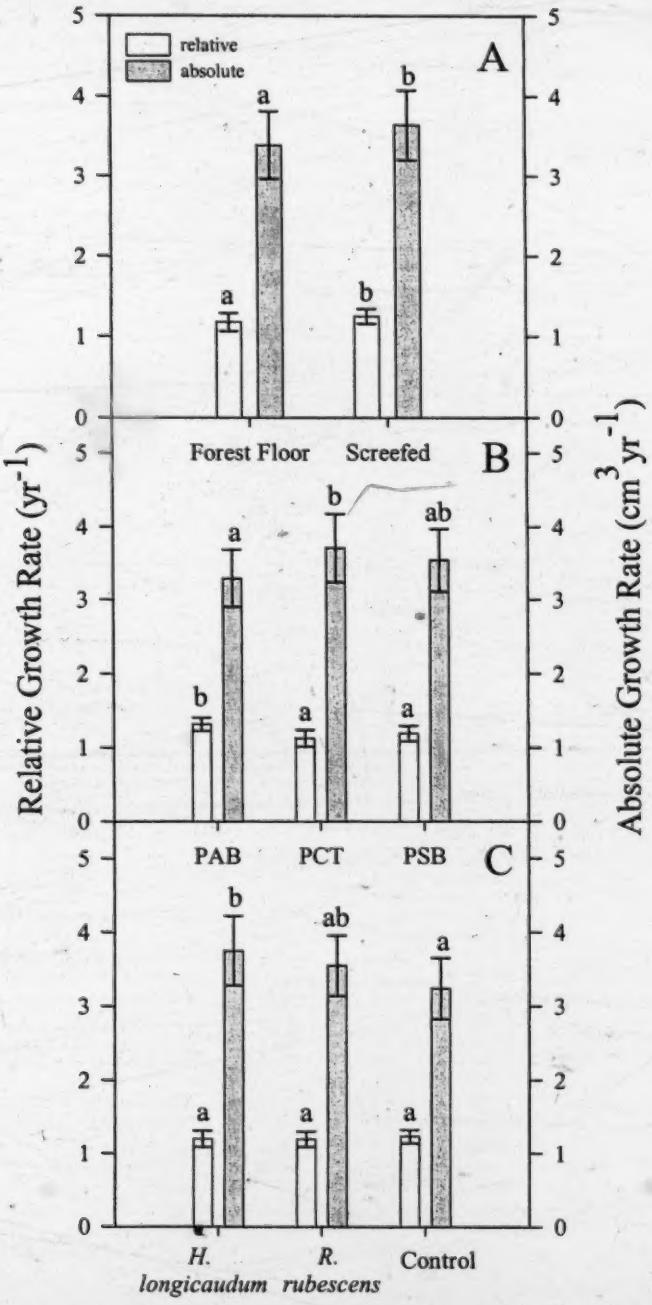


Figure 3-2: Growth rates of seedlings outplanted at the Graham River following two seasons of growth: A-seedlings planted into either manually screefed planting spots or directly onto the forest floor; B- seedlings grown in AirBlocks™ (PAB), Copperblocks™ (PCT), or Styroblocks™ (PSB); C- seedlings inoculated with *Hebeloma longicaudum*, *Rhizopogon rubescens*, or left as non-inoculated controls. Different letters associated with different bars indicate a significant difference within a category (multiple comparison *t*-tests, Tukey's *W*, α=0.05), mean values are shown ± 1SE, n=20.

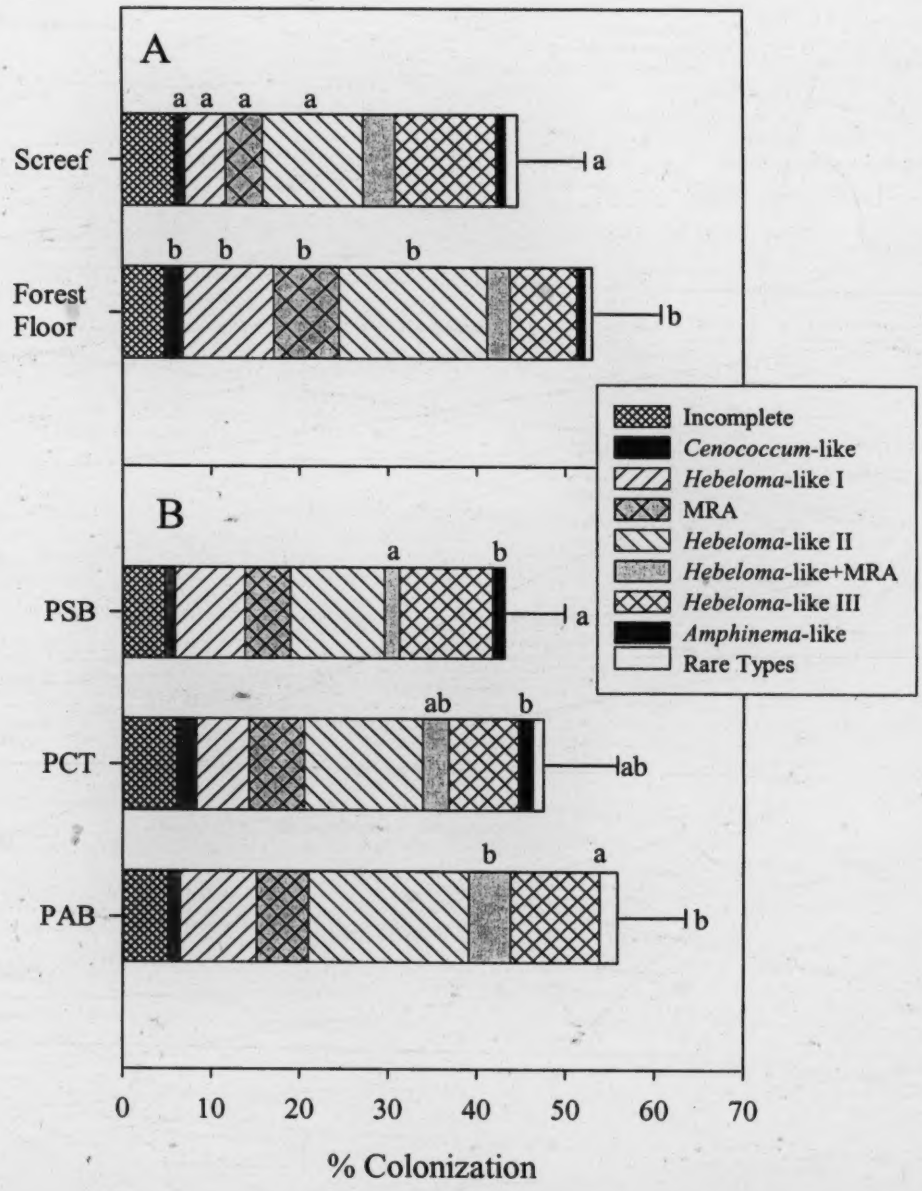


Figure 3-3: Relative abundance of the most common ectomycorrhizal morphotypes and overall percent colonization of root tips for: A-seedlings planted into either manually screefed planting spots, or planted directly into the forest floor; B- seedlings grown in AirBlocks™ (PAB), Copperblocks™ (PCT), or Styroblocks™ (PSB); after two seasons of growth in the field. Different letters associated with different morphotypes indicate a significant difference in mean relative abundance of the ectomycorrhizal morphotype between planting methods (multiple comparison *t*-tests, α=0.05, n=6), or between container types (Tukey's *W*, α=0.05, n=6).

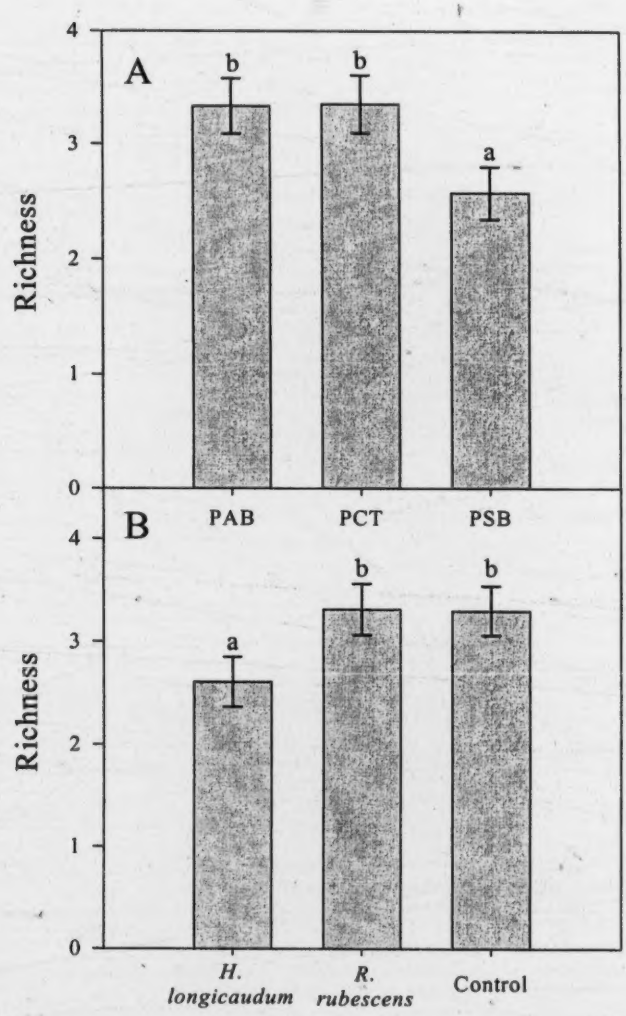


Figure 3-4: Ectomycorrhizal richness of colonized root tips of seedlings: A-grown in AirBlocks™ (PAB), Copperblocks™ (PCT), and Styroblocks™ (PSB); B- inoculated with either *H. longicaudum* or *R. rubescens* or left as non-inoculated control seedlings; after two seasons of growth in the field. Different letters associated with bars indicates a significant difference between values (Tukey's *W*, α=0.05). Bars represent overall mean values per seedling and are shown ± 1SE, n=6.

Chapter 4

General Discussion and Conclusions

Container Type

The results of the two studies presented in this thesis provide no substantial evidence to support the superiority of any of the studied container types for lodgepole pine seedling production in the nursery. Prior to planting, Copperblock™ and Styroblock™ seedlings surpassed AirBlock™ seedlings in terms of seedling size for spring-planted stock (Chapter 2). This was, however, most likely due to the inadequate irrigation supplied for the AirBlock™ seedlings, as all container types received the same amount of water in this experiment. AirBlocks™ require more irrigation (Lamhamedi *et al.* 2001) than Styroblocks™ and Copperblocks™ because they are made of hard plastic with many side slits; therefore, the potting substrate becomes hotter and drier than with Styrofoam block-style containers. Summer-plant AirBlock™ seedlings were supplied with adequate irrigation, and did not differ in size from seedlings grown in the other two containers (Chapter 3).

Although growth in the nursery is important, it is the performance of seedlings once planted in the field that is paramount. Over the first two years Copperblock™ spring-planted seedlings outperformed Styroblock™ seedlings, which in turn outperformed AirBlock™ seedlings (Chapter 2). Copperblock™ seedlings were larger at planting and continued to exhibit greater absolute growth (on average by 56% over Styroblock™ and AirBlock™ seedlings), while AirBlock™ seedlings exhibited the

highest relative growth rates (18% over Styroblock™). Differences were smaller amongst summer-planted seedlings (Chapter 3). The summer-plant Copperblock™ and Styroblock™ stock did not differ in size, but the Copperblock™ seedlings were still significantly larger than the AirBlock™ seedlings after two seasons growth in the field. AirBlock™ seedlings exhibited the greatest relative growth rates (on average by 14% over Copperblock™ and Styroblock™ seedlings), while Copperblock™ seedlings exhibited the greatest absolute growth rates (by 13% over AirBlock™ seedlings). Results here indicate that the emergent root growth of both AirBlock™ and Copperblock™-grown lodgepole pine seedlings tends to be more evenly distributed over the entire surface of the root plug, and occur more from the upper portions of the root plug, when compared to conventional Styroblock™-grown seedlings. Therefore copper-pruned seedlings tend to more accurately mimic natural root system establishment patterns. Results here are consistent with other recent studies in which copper root pruning (Ruehle 1985; Dunn *et al.* 1997; Aldrete *et al.* 2002) of container-grown seedlings resulted in a more fibrous and well developed root system.

AirBlock™-grown seedlings did not perform as expected over the first two years in the field. Air pruning has been shown to produce fibrous robust root systems (Lamhamedi *et al.* 2001; Gingras *et al.* 2002; Jones *et al.* 2002), and, therefore, could function as an alternative to copper root pruning. It was expected therefore, that AirBlock™ stock would have similar field performance characteristics to the Copperblock™ stock. Therefore, it was surprising that AirBlock™ stock was smaller than the other stock types after both seasons in the field for both the spring plant and summer plant trials. For the spring plant trial, this was due to size differences that

developed in the nursery, but for the summer plant trial, the differences developed in the field. Although smaller in size than the other stock types, AirBlock™ stock exhibited the largest absolute growth for the summer planted stock, and surpassed Styroblock™ stock for the spring planted stock. Thus, differences in seedling height and diameter will likely be small over the long term. If these trends continue the AirBlock™ stock will equal or surpass Styroblock™ stock after three growing seasons. These plots will be measured in future years to determine if this difference in increment continues.

Ectomycorrhizal Fungal Inoculation

Inoculation of lodgepole pine seedlings in the nursery with ectomycorrhizal fungi produced mixed results. At lifting, no significant differences in seedling size were noted between inoculated and non-inoculated seedlings, for spring-planted stock (Chapter 2). However these results may possibly have been influenced by the fact that water was limiting for the spring-plant AirBlock™ seedlings. Additionally inoculation in the nursery failed to affect spring-planted seedling field growth. Inoculated summer-plant seedlings were, however, considerably larger than non-inoculated seedlings at lifting (Chapter 3). Since growth in the nursery occurs under ideal conditions, with nutrients and water supplied in excess, growth stimulation in the nursery in response to inoculation, is not necessarily expected (Stenström 1990; Villeneuve *et al.* 1991; Quoreshi & Timmer 2000). However, as results here indicate, inoculation of seedlings with ectomycorrhizal fungi has the potential to assist in the production of a larger seedling.

Inoculation of seedlings while in the nursery significantly affected summer planted stock only (Chapter 3). Moreover, inoculated seedlings were larger at lifting (by 14%) and continued to exhibit greater stem volume (by 13%) after each year's growth in the field. No difference was noted however with respect to the relative growth rates of seedlings, indicating that the increased size of inoculated seedlings was related to effects in the nursery. Differences in seedling response to inoculation could be attributed to the success or failure of inoculation in the nursery. In either experiment, percent colonization of inoculated seedlings did not differ significantly at lifting from controls, however summer-plant seedlings were on average colonized to a greater extent than were spring-plant seedlings. Therefore differences in root system colonization levels may explain the increased growth of summer-plant seedlings as increased growth has been correlated with higher rates of colonization (Thomson *et al.* 1994; Scagel & Linderman 1998). Additionally seedling growth response to inoculation in the nursery may be affected by factors such as seed lot and seed source (Folk *et al.* 1999), as well as phenological differences in lodgepole pine provenances (Chuine *et al.* 2001).

Laboratory and field studies have illustrated the potential benefits of the inoculation of seedlings with specific ectomycorrhizal fungi (Castellano *et al.* 1985; Walker 1999; Parladé *et al.* 2001), especially under stressful conditions. However some studies signify no potential benefit of inoculation (Bledsoe *et al.* 1982; Loopstra *et al.* 1988; Cram *et al.* 1999)). In the field, inoculation often increases survival or growth under drought conditions (Valdés 1986; Letho 1992; Browning & Whitney 1993). For example, Browning and Whitney (1992) conclude that the growth and nutrition following outplanting, of *Pinus banksiana* and *Picea mariana,* can be improved through

inoculation with ectomycorrhizal fungi in the nursery. MacFall and Slack (1991) report that inoculated container-grown *Pinus resinosa* seedlings were 28% taller than non-inoculated controls, and inoculation significantly increased survival following outplanting. Querejeta *et al.* (1998) showed that ectomycorrhizal *Pinus halepensis,* outplanted in a semi-arid site, exhibited an increase in growth of short lateral roots coupled with an increase in drought tolerance over non-mycorrhizal controls. Obviously, rapid early root growth is critical for the establishment of outplanted seedlings (Ritchie & Dunlap 1980; Burdett *et al.* 1983; Balisky *et al.* 1995), which is especially true for seedlings that are exposed to periods of water deficit. Potential extraction of water from a deeper and wider soil profile, together with earlier access to water, has the potential to allocate ectomycorrhizal conifer seedlings with a distinct advantage with respect to outplanting success. These potential benefits would be of even greater significance in many regions, such as the interior of British Columbia, where extended periods of water deficit are common. Nursery effects, such as inoculation, are often short-lived. Further measurement will determine whether the slight increase in growth produced by inoculation justifies the additional expenditure of fungal inoculation.

Landing Rehabilitation

As previously stated, growth in the nursery occurs under ideal conditions, and many factors have the potential to affect the physiology and morphology of commercially produced conifer seedlings. Although certain factors can be controlled or eliminated while in the nursery, the overriding factor responsible for success after

planting is the planting microsite environment (Grossnickle & Heikurinen 1989; Simpson & Vyse 1995; Delong *et al.* 1997). Root morphology is extensively influenced by site conditions (Balisky *et al.* 1995; Krasowski & Owens 2000), illustrating the importance of site preparation. In the British Columbian interior landings occupy a significant portion of the harvested area within the operational forest (Bulmer & Curran 1999). Therefore a significant increase in the amount of land regenerating as future productive forest would be achieved, if landings could be successfully rehabilitated.

Results here indicate that landing rehabilitation, through the incorporation of recovered topsoil and burn-pile debris, via mechanical tilling, provides an adequate rooting environment for successful reforestation. Seedlings planted in the landing plots receiving topsoil and burn-pile debris were 60% larger and more vigorous after two years growth, exhibiting 78% greater absolute growth rates and 27% greater relative growth rates, than seedlings planted in the adjacent cutblocks. Restoration of degraded forest soils requires alleviation of the conditions limiting site productivity (Bulmer 1998). Although results here indicated increased site productivity over the adjacent cutblock, it should be noted however that the initial enhanced growth effects (2 years) of seedlings possibly could diminish over time.

Forest Floor Planting

Planting lodgepole pine seedlings directly into the forest floor should be considered as an alternative to manual spot screefing, and potentially to mechanical screefing. Although various site conditions may favour screefing, such as excessive

vegetative competition (Cain 1996; Simard *et al.* 2003) or sub-optimal soil temperature (Delong *et al.* 1997), the added expense of screefing may not be warranted against only marginal differences in seedling above ground growth response. Although seedlings planted in screefed spots exhibited slightly greater growth rates and were somewhat larger, these differences are unlikely to increase further due to the small size of the manually screefed patches. Additionally, although seedlings planted in screefed planting sites exhibited greater above ground growth, seedlings planted in the forest floor exhibited greater below ground growth. Moreover, there was no difference noted with respect to shoot dry mass, root dry mass, or whole seedling dry mass. Thus indicating differences in the allocation of metabolic reserves, as forest floor planted seedlings produced an increased number of finer roots, while screef planted seedlings produced more slender stem growth.

Soil temperatures, below those conducive for optimal root growth, will have a negative influence on seedling growth (Sutton 1991; Bulmer 2000). The practice of screefing away (removing) forest floor materials, to expose mineral soil, thus aid in warming the mineral soil and promote root growth, may be beneficial at first glance, but does not account for one major factor: roots grow in the forest floor, especially the lower layers near the mineral soil interface (Eis 1974; Eis 1978; Balisky *et al.* 1995). Thus the concept of screefing away all the forest floor material to warm the mineral soil, would be the best option, if roots did not grow in the forest floor. Additionally, how much warmer is spot screefed mineral soil than undisturbed forest floor? The presumption that spot screefing increases the temperature of the rooting substrate by some amount (i.e. by X °C) over the forest floor, and hence potentially enhances root growth, is not precisely

accurate. If the organic horizons had not been removed by screefing, root growth would occur in the warmer forest floor horizons, as well as the lower mineral soil, had the forest floor not been previously removed. Moreover, the forest floor can potentially provide and ideal rooting environment, with abundant sources of ectomycorrhizal inoculum, illustrated here by significant increases in ectomycorrhizal colonization and root growth.

Management Implications

Container Type

In the experiments presented here, I did not find sufficient evidence to support the universal use of one container type over another for the production of interior lodgepole pine in the nursery. The use of Copperblock™ stock may be warranted on sites with periods of water deficit. Copperblock™ seedlings continued to have higher absolute growth rates than other container types for spring-planted stock at a drought-prone site (IDF dk2). Additionally, Copperblock™ stock exhibited greater absolute growth for summer-planted stock, indicating the use of Copperblock™ stock may be warranted for cool wet locations (ESSF mv2). Additionally, based on early growth results, these trials suggest no benefit to the use of the AirBlock™ container over Styroblock™ containers for the production of interior lodgepole pine, and it is too early to know whether they will influence future tree stability. AirBlock™ stock exhibited greater relative growth rates, although of lesser seedling volume after the second season, indicating this stock type may require additional time to establish.

Fungal Inoculation

It is still not clear whether the inoculation of seedlings with commercially available ectomycorrhizal fungi in the nursery imparts an advantage after outplanting during normal forestry operations in Canada. The minor growth response observed in one of the experiments presented here may not justify the additional cost of inoculating seedlings. Inoculated summer-planted seedlings were considerably taller than non-inoculated seedlings at lifting and, although these differences were still evident after 2 years of field growth, relative growth rates did not differ between inoculated and non-inoculated seedlings. Further measurement will determine whether the slight increase in growth produced by inoculation justifies the additional expenditure of approximately 8% per seedling (inoculation increases average cost of a seedling from $0.25 to $0.27).

Landing Rehabilitation

Results indicate that landing rehabilitation, through the incorporation of recovered topsoil and burn-pile debris via mechanical tilling, provides an adequate rooting environment for successful reforestation. In this experiment after two seasons growth, seedlings planted on fully rehabilitated landings were substantially larger exhibiting significantly greater growth rates, compared to seedlings in the adjacent cutblocks. Moreover, the extra expense associated with incorporating topsoil, ash, and burn-pile debris, led to significantly improved growth compared with simply tilling the landings. Due to the high costs associated with mechanical site preparation, cost-

effective soil rehabilitation will likely require innovative strategies for conserving topsoil during landing construction, and distributing topsoil and burn-pile debris during rehabilitation.

Forest Floor Planting

Decisions regarding forest floor planting must be site-specific and depend upon the anticipated severity of factors potentially limiting initial seedling growth. If severe limiting factors are not anticipated, forest floor planting should be considered as an alternative to spot screefing. After 2 years growth, seedlings planted in screefed planting spots were only slightly larger in stem volume than seedlings planted directly in the forest floor; however, seedlings planted in the forest floor produced a greater number of roots. Differences are unlikely to increase further due to the small size of the manually screefed planting spots.

Future Research

The two studies presented assessed early growth and performance, and ectomycorrhizal status of interior lodgepole pine. These field trials must be revisited periodically in the future to assess the potential long term treatment effects upon tree physiology and morphology, stand dynamics and development, and stand rotation. Both studies presented in this thesis describe significant treatment effects with respect to early plantation establishment, however many factors can potentially influence growth and

performance after initial successful establishment. Additionally, both landing rehabilitation and forest floor planting should be investigated across a wide spectrum of site characteristics and with different planting stock types of different species.

Many studies have shown the potential benefits of chemical root pruning of nursery stock, however there is a lack of research regarding plantation growth after initial establishment. Additionally, very few studies have investigated the potential effects of air-pruned root systems on plantation growth. Further field trials are therefore needed to assess the growth and performance of nursery stock grown in different containers and outplanted across a variety of sites.

Although there is an increasing amount of evidence detailing the potential benefits of ectomycorrhiza formation with respect to conifer seedlings, the advantage of inoculation in the nursery remains to be shown. Conifer seedlings, especially lodgepole pine, frequently become colonized in the nursery, without inoculation. Additionally, these seedling root systems undergo fungal succession once planted out as root systems become colonized with native ectomycorrhizal fungi. This promotes the hypothesis that inoculation of seedlings with native ectomycorrhizal fungal community members, from the specific site seedlings are destined to be planted, may provide a distinct advantage.

Literature Cited

Aldrete, A., Mexal, J.G., Phillips, R., and Vallotton, A.D. 2002. Copper coated polybags improve seedling morphology for two nursery-grown Mexican pine species. For. Ecol. Manage. 163: 197-204.

Balisky, A.C., Salonius, P., Walli, C., and Brinkman, D. 1995. Seedling roots and forest floor: misplaced and neglected aspects of British Columbia's reforestation effort? For. Chron. 71: 59-65.

Bledsoe, C.S., Tennyson, K., and Lopushinsky, W. 1982. Survival and growth of outplanted Douglas fir seedlings inoculated with mycorrhizal fungi. Can. J. For. Res. 12: 720-723.

Browning, M.H.R. and Whitney, R.D. 1993. Infection of containerized jack pine and black spruce seedlings by *Laccaria* species and *Thelephora terrestris* and seedling survival and growth after outplanting. Can. J. For. Res. 23: 330-333.

Bulmer, C. 2000. Reclamation of forest soils with excavator tillage and organic amendments. For. Ecol. Manage. 133: 157-163.

Bulmer, C.E. 1998. Forest soil rehabilitation in British Columbia: a problem analysis. B.C. Ministry of Forests. Land Management Handbook. Victoria, B.C. Rep. LMH-44.

Bulmer, C.E. and Curran, M. 1999. Retrospective evaluation of log landing rehabilitation on coarser textured soils in southeastern British Columbia. B.C. Ministry of Forests. Extension Note. Victoria, B.C. Rep. EN-042.

Burdett, A.N., Simpson, D.G., and Thompson, C.F. 1983. Root development and plantation establishment success. Plant Soil 71: 103-110.

Cain, M.D. 1996. Woody and herbaceous competition effects on the growth of naturally regenerated loblolly pine and shortleaf pines through 11 years. New For. 14: 107-125.

Castellano, M.A., Trappe, J.M., and Molina, R. 1985. Inoculation of container-grown Douglas fir seedlings with basidiospores of *Rhizopogon vinicolor* and *R. colossus*: effects of fertility and spore application rate. Can. J. For. Res. 15: 10-13.

Chuine, I., Aitken, S.N., and Ying, C.C. 2001. Temperature thresholds of shoot elongation in provenances of *Pinus contorta*. Can. J. For. Res. 31: 1444-1455.

Cram, M.M., Mexal, J.G., and Souter, R. 1999. Successful reforestation of South Carolina sandhills is not influenced by seedling inoculation with *Pisolithus tinctorius* in the nursery. South. J. Appl. For. 23: 46-51.

Delong, H.B., Lieffers, V.J., and Blenis, P.V. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. 27: 1452-1457.

Dunn, G.M., Huth, J.R., and Lewty, M.J. 1997. Coating nursery containers with copper carbonate improves root morphology of five native Australian tree species used in agroforestry systems. Agroforest. Syst. 37: 143-155.

Eis, S. 1974. Root system morphology of western hemlock, western red cedar and Douglas fir. Can. J. For. Res. 4: 28-38.

Eis, S. 1978. Natural root forms of western conifers. *In* Proc. Proceedings of the root form of planted trees symposium, May 16-19, 1978. Victoria, B.C. *Edited by* E. van Eerden and J. M. Kinghorn. British Columbia Ministry of Forests / Canadian Forest Service, Joint Report No. 8. pp. 23-27.

Folk, R.S., Grossnickle, S.C., Axelrood, P., and Trotter, D. 1999. Seed lot, nursery, and bud dormancy effects on root electrolyte leakage of Douglas-fir (*Pseudotsuga menziesii*) seedlings. Can. J. For. Res. 29: 1269-1281.

Gingras, B.M., Richard, S., and Robert, N. 2002. Comparative performance after five years of large sized conifers and broadleaves grown in air-slit containers. Direction de la Recherche Forestiere, Ministere des Ressources Naturelles. Sainte Foy, Quebec. Rep. No. 141.

Grossnickle, S.C. and Heikurinen, J. 1989. Site preparation: water relations and growth of newly planted jack pine and white spruce. New For. 3: 99-123.

Jones, M.D., Kiiskila, S., and Flanagan, A. 2002. Field performance of pine stock types: Two-year results of a trial on interior lodgepole pine seedlings grown in Styroblocks™, Copperblocks™, or Airblocks™. B.C. J. Ecosys. Manage. 2: 59-70.

Krasowski, M.J. and Owens, J.N. 2000. Morphological and physiological attributes of root systems and seedling growth in three different *Picea glauca* reforestation stock. Can. J. For. Res. 30: 1669-1681.

Lamhamedi, M., Lambany, G., Margolis, H., Renaud, M., Veilleux, L., and Bernier, P.Y. 2001. Growth, physiology, and leachate losses in *Picea glauca* seedlings (1+0) grown in air-slit containers under different irrigation regimes. Can. J. For. Res. 31: 1968-1980.

Letho, T. 1992. Effect of drought on *Picea sitchensis* seedlings inoculated with mycorrhizal fungi. Scand. J. For. Res. 7: 177-182.

Loopstra, E.M., Shaw, C.G.I., and Sidle, R.C. 1988. Ectomycorrhizal inoculation fails to improve performance of sitka spruce seedlings on clearcuts in southeastern Alaska. West. J. Appl. For. 3: 110-112.

Parladé, J., Cohen, M., Doltra, J., Luque, J., and Pera, J. 2001. Continuous measurement of stem-diameter growth response of *Pinus pinea* seedlings mycorrhizal with *Rhizopogon roseolus* and submitted to two water regimes. Mycorrhiza 11: 129-136.

Querejeta, J.I., Roldán, A., Albaladejo, J., and Castillo, V. 1998. The role of mycorrhizae, site preparation, and organic amendment in the afforestation of a semi-arid Mediterranean site with *Pinus halepensis*. For. Sci. 44: 203-211.

Quoreshi, A.M. and Timmer, V.R. 2000. Early outplanting performance of nutrient-loaded containerized black spruce seedlings inoculated with *Laccaria bicolor*: a bioassay study. Can. J. For. Res. 30: 744-752.

Ritchie, G.A. and Dunlap, J.R. 1980. Root growth potential: its development and expression in forest tree seedlings. N. Z. J. For. Sci. 10: 218-248.

Ruehle, J.L. 1985. The effect of cupric carbonate on root morphology of containerized mycorrhizal pine seedlings. Can. J. For. Res. 15: 586-592.

Scagel, C.F. and Linderman, R.G. 1998. Influence of ectomycorrhizal fungal inoculation on growth and root IAA concentrations of transplanted conifers. Tree Phys. 18: 739-747.

Simard, S.W., Jones, M.D., Durall, D.M., Hope, G.D., Stathers, R.J., Sorensen, N.S., and Ziomonick, B.J. 2003. Chemical and mechanical site preparation: effects on *Pinus contorta* growth, physiology, and micro-site quality on steep forest sites in British Columbia. Can. J. For. Res. 33: 1495-1515.

Simpson, D.G. and Vyse, A. 1995. Planting stock performance: site and RGP effects. For. Chron. 71: 739-742.

Stenström, E. 1990. Variation in the field response of *Pinus sylvestris* to nursery inoculation with four different ectomycorrhizal fungi. Can. J. For. Res. 20: 1796-1803.

Sutton, R.F. 1991. Soil properties and root development in forest trees: A review. Forestry Canada. Sault Ste. Marie, Ont. Information Report O-X-413.

Thomson, B.D., Grove, T.S., Malajczuk, N., and Hardy, G.E.S. 1994. The effectiveness of ectomycorrhizal fungi in increasing the growth of *Eucalyptus globulus* Labill. in relation to root colonization and hyphal development in soil. New Phytol. 126: 517-524.

Valdés, M. 1986. Survival and growth of pines with specific ectomycorrhizae after 3 years on a highly eroded site. Can. J. Bot. 64: 885-888.

Villeneuve, N., Tacon, F.l., and Bouchard, D. 1991. Survival of inoculated *Laccaria bicolor* in competition with native ectomycorrhizal fungi and effects on the growth of outplanted Douglas-fir seedlings. Plant Soil 135: 95-107.

Walker, R.F. 1999. Reforestation of an eastern Sierra Nevada surface mine with containerized jeffrey pine: seedling growth and nutritional responses to controlled release fertilization and ectomycorrhizal inoculation . J. Sustain. For. 9: 127-147.

Appendix I

This appendix contains the results of the analysis of variance to accompany Chapter 2.

Tables have been abbreviated to exclude site effects, and multi-way interactions.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Root Viability (TTC)	.005(a)	1	.005	.726	.399
	RGC - top	50.317(b)	1	50.317	2.483	.123
	RGC - middle	7.826(c)	1	7.826	.112	.740
	RGC - bottom	338.349(d)	1	338.349	.465	.499
	RGC - total	72.306(e)	1	72.306	.065	.799
	Roots % Injury	505.094(f)	1	505.094	2.242	.142
	Needles % Injury	173.105(g)	1	173.105	.419	.521
	Total Nonstructural Carbohydrate	.108(h)	1	.108	.007	.932
Intercept	Root Viability (TTC)	2.615	1	2.615	415.046	.000
	RGC - top	1397.746	1	1397.746	68.968	.000
	RGC - middle	5317.350	1	5317.350	75.792	.000
	RGC - bottom	57166.921	1	57166.921	78.507	.000
	RGC - total	122082.211	1	122082.211	110.541	.000
	Roots % Injury	47649.460	1	47649.460	211.484	.000
	Needles % Injury	134930.989	1	134930.989	326.910	.000
	Total Nonstructural Carbohydrate	5670.810	1	5670.810	384.072	.000
SL	Root Viability (TTC)	.005	1	.005	.726	.399
	RGC - top	50.317	1	50.317	2.483	.123
	RGC - middle	7.826	1	7.826	.112	.740
	RGC - bottom	338.349	1	338.349	.465	.499
	RGC - total	72.306	1	72.306	.065	.799
	Roots % Injury	505.094	1	505.094	2.242	.142
	Needles % Injury	173.105	1	173.105	.419	.521
	Total Nonstructural Carbohydrate	.108	1	.108	.007	.932
Error	Root Viability (TTC)	.252	40	.006		
	RGC - top	810.659	40	20.266		
	RGC - middle	2806.293	40	70.157		
	RGC - bottom	29126.984	40	728.175		
	RGC - total	44176.265	40	1104.407		
	Roots % Injury	9012.380	40	225.310		
	Needles % Injury	16509.865	40	412.747		
	Total Nonstructural Carbohydrate	590.599	40	14.765		
Total	Root Viability (TTC)	2.916	42			
	RGC - top	2221.000	42			
	RGC - middle	8141.000	42			
	RGC - bottom	88004.000	42			
	RGC - total	168020.000	42			
	Roots % Injury	56664.706	42			
	Needles % Injury	151921.626	42			

	Total Nonstructural Carbohydrate	6318.192	42			
Corrected Total	Root Viability (TTC)	.257	41			
	RGC - top	860.976	41			
	RGC - middle	2814.119	41			
	RGC - bottom	29465.333	41			
	RGC - total	44248.571	41			
	Roots % Injury	9517.475	41			
	Needles % Injury	16682.969	41			
	Total Nonstructural Carbohydrate	590.708	41			

Will Lake: Seedling Assessment at Lifting

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	# roots top	1166.250(a)	8	145.781	2.770	.011
	# roots middle	2319.500(b)	8	289.937	2.782	.011
	# roots bottom	15261.194(c)	8	1907.649	4.131	.001
	Total # roots	39471.694(d)	8	4933.962	6.151	.000
	% roots top	2419.433(e)	8	302.429	4.262	.000
	% roots middle	4308.837(f)	8	538.605	3.786	.001
	% roots bottom	36983.173(g)	8	4622.897	1.532	.164
	seedling height	211.153(h)	8	26.394	8.019	.000
	seedling diameter	1.914(i)	8	.239	.999	.446
	seedling volume	5.701(j)	8	.713	3.409	.003
Intercept	# roots top	3872.000	1	3872.000	73.569	.000
	# roots middle	12168.000	1	12168.000	116.742	.000
	# roots bottom	101400.056	1	101400.056	219.596	.000
	Total # roots	226016.056	1	226016.056	281.758	.000
	% roots top	10430.494	1	10430.494	147.005	.000
	% roots middle	39044.288	1	39044.288	274.437	.000
	% roots bottom	404583.107	1	404583.107	134.037	.000
	seedling height	7371.003	1	7371.003	2239.306	.000
	seedling diameter	858.361	1	858.361	3584.800	.000
	seedling volume	114.141	1	114.141	546.035	.000
CONT	# roots top	576.083	2	288.042	5.473	.006
	# roots middle	1208.083	2	604.042	5.795	.005
	# roots bottom	7774.361	2	3887.181	8.418	.001
	Total # roots	9867.528	2	4933.764	6.151	.004
	% roots top	1891.375	2	945.688	13.328	.000
	% roots middle	3675.453	2	1837.727	12.917	.000
	% roots bottom	15493.122	2	7746.561	2.566	.085
	seedling height	175.124	2	87.562	26.601	.000
	seedling diameter	1.132	2	.566	2.364	.102
	seedling volume	4.741	2	2.370	11.339	.000
INOC	# roots top	157.000	2	78.500	1.492	.233

	# roots middle	405.583	2	202.792	1.946	.151
	# roots bottom	1607.694	2	803.847	1.741	.184
	Total # roots	9143.694	2	4571.847	5.699	.005
	% roots top	38.464	2	19.232	.271	.763
	% roots middle	328.005	2	164.003	1.153	.322
	% roots bottom	6942.563	2	3471.281	1.150	.323
	seedling height	16.334	2	8.167	2.481	.092
	seedling diameter	.042	2	.021	.088	.916
	seedling volume	.452	2	.226	1.080	.346
CONT * INOC	# roots top	433.167	4	108.292	2.058	.097
	# roots middle	705.833	4	176.458	1.693	.163
	# roots bottom	5879.139	4	1469.785	3.183	.019
	Total # roots	20460.472	4	5115.118	6.377	.000
	% roots top	489.594	4	122.398	1.725	.156
	% roots middle	305.378	4	76.344	.537	.709
	% roots bottom	14547.488	4	3636.872	1.205	.318
	seedling height	19.694	4	4.923	1.496	.214
	seedling diameter	.741	4	.185	.773	.547
	seedling volume	.509	4	.127	.608	.658
Error	# roots top	3315.750	63	52.631		
	# roots middle	6566.500	63	104.230		
	# roots bottom	29090.750	63	461.758		
	Total # roots	50536.250	63	802.163		
	% roots top	4470.073	63	70.954		
	% roots middle	8963.053	63	142.271		
	% roots bottom	190162.553	63	3018.453		
	seedling height	207.374	63	3.292		
	seedling diameter	15.085	63	.239		
	seedling volume	13.169	63	.209		
Total	# roots top	8354.000	72			
	# roots middle	21054.000	72			
	# roots bottom	145752.000	72			
	Total # roots	316024.000	72			
	% roots top	17320.000	72			
	% roots middle	52316.178	72			
	% roots bottom	631728.833	72			
	seedling height	7789.530	72			
	seedling diameter	875.360	72			
	seedling volume	133.011	72			
Corrected Total	# roots top	4482.000	71			
	# roots middle	8886.000	71			
	# roots bottom	44351.944	71			
	Total # roots	90007.944	71			
	% roots top	6889.506	71			
	% roots middle	13271.890	71			
	% roots bottom	227145.726	71			
	seedling height	418.527	71			

seedling diameter	16.999	71			
seedling volume	18.870	71			

Will Lake: % Colonization at Lifting

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	33100.275(a)	8	4137.534	5.388	.000
Intercept	199912.264	1	199912.264	260.334	.000
CONT	3427.610	2	1713.805	2.232	.114
INOC	427.510	2	213.755	.278	.758
CONT * INOC	29245.154	4	7311.289	9.521	.000
Error	62200.462	81	767.907		
Total	295213.000	90			
Corrected Total	95300.737	89			

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Height 2000	10863.876(a)	80	135.798	8.840	.000
	Height 2001	25118.035(b)	80	313.975	9.033	.000
	delta Height	11053.844(c)	80	138.173	7.652	.000
	DGL 2000	232.066(d)	80	2.901	5.311	.000
	DGL 2001	3958.712(e)	80	49.484	14.099	.000
	delta DGL	3129.398(f)	80	39.117	12.477	.000
	Seedling Volume 2000	899.000(g)	80	11.238	6.265	.000
	Seedling Volume 2001	125799.878(h)	80	1572.498	9.687	.000
	Absolute Growth Rate	116015.457(i)	80	1450.193	9.509	.000
	Relative Growth Rate	323.439(j)	80	4.043	10.718	.000
	Seedling Vigor	75.262(k)	80	.941	2.482	.000
Intercept	Height 2000	384503.760	1	384503.760	25029.024	.000
	Height 2001	809248.818	1	809248.818	23280.656	.000
	delta Height	78119.640	1	78119.640	4326.460	.000
	DGL 2000	18577.065	1	18577.065	34013.177	.000
	DGL 2001	61353.566	1	61353.566	17481.359	.000
	delta DGL	12409.696	1	12409.696	3958.294	.000
	Seedling Volume 2000	9790.796	1	9790.796	5458.586	.000
	Seedling Volume 2001	309114.247	1	309114.247	1904.263	.000
	Absolute Growth Rate	208878.572	1	208878.572	1369.658	.000
	Relative Growth Rate	2824.462	1	2824.462	7487.729	.000
	Seedling Vigor	6174.941	1	6174.941	16288.967	.000
TREAT	Height 2000	3698.319	2	1849.159	120.370	.000
	Height 2001	11749.233	2	5874.617	169.002	.000
	delta Height	3898.676	2	1949.338	107.959	.000
	DGL 2000	20.724	2	10.362	18.972	.000
	DGL 2001	1551.959	2	775.979	221.098	.000
	delta DGL	1218.192	2	609.096	194.282	.000
	Seedling Volume 2000	100.761	2	50.381	28.088	.000
	Seedling Volume 2001	43391.822	2	21695.911	133.655	.000
	Absolute Growth Rate	40490.842	2	20245.421	132.753	.000
	Relative Growth Rate	112.038	2	56.019	148.508	.000
	Seedling Vigor	5.391	2	2.695	7.110	.001
CONT	Height 2000	2708.316	2	1354.158	88.148	.000
	Height 2001	2933.178	2	1466.589	42.191	.000
	delta Height	8.030	2	4.015	.222	.801
	DGL 2000	134.798	2	67.399	123.402	.000
	DGL 2001	331.111	2	165.555	47.171	.000
	delta DGL	112.508	2	56.254	17.943	.000
	Seedling Volume 2000	504.050	2	252.025	140.510	.000
	Seedling Volume 2001	13247.173	2	6623.587	40.804	.000
	Absolute Growth Rate	9407.750	2	4703.875	30.844	.000

	Relative Growth Rate	9.782	2	4.891	12.966	.000
	Seedling Vigor	.476	2	.238	.628	.534
INOC	Height 2000	49.074	2	24.537	1.597	.203
	Height 2001	216.860	2	108.430	3.119	.045
	delta Height	65.652	2	32.826	1.818	.163
	DGL 2000	1.221	2	.611	1.118	.327
	DGL 2001	8.738	2	4.369	1.245	.288
	delta DGL	7.907	2	3.953	1.261	.284
	Seedling Volume 2000	8.829	2	4.415	2.461	.086
	Seedling Volume 2001	279.706	2	139.853	.862	.423
	Absolute Growth Rate	280.939	2	140.469	.921	.398
	Relative Growth Rate	.594	2	.297	.788	.455
	Seedling Vigor	.212	2	.106	.280	.756
TREAT * CONT	Height 2000	32.587	4	8.147	.530	.713
	Height 2001	20.772	4	5.193	.149	.963
	delta Height	16.585	4	4.146	.230	.922
	DGL 2000	3.596	4	.899	1.646	.160
	DGL 2001	85.773	4	21.443	6.110	.000
	delta DGL	75.474	4	18.868	6.018	.000
	Seedling Volume 2000	19.420	4	4.855	2.707	.029
	Seedling Volume 2001	4597.215	4	1149.304	7.080	.000
	Absolute Growth Rate	4251.063	4	1062.766	6.969	.000
	Relative Growth Rate	2.249	4	.562	1.490	.203
	Seedling Vigor	2.847	4	.712	1.878	.112
TREAT * INOC	Height 2000	81.302	4	20.325	1.323	.259
	Height 2001	74.281	4	18.570	.534	.711
	delta Height	152.793	4	38.198	2.116	.077
	DGL 2000	1.880	4	.470	.861	.487
	DGL 2001	5.811	4	1.453	.414	.799
	delta DGL	9.032	4	2.258	.720	.578
	Seedling Volume 2000	13.494	4	3.373	1.881	.111
	Seedling Volume 2001	502.265	4	125.566	.774	.542
	Absolute Growth Rate	498.245	4	124.561	.817	.514
	Relative Growth Rate	3.192	4	.798	2.115	.077
	Seedling Vigor	3.402	4	.850	2.243	.062
CONT * INOC	Height 2000	55.760	4	13.940	.907	.459
	Height 2001	224.621	4	56.155	1.615	.168
	delta Height	174.222	4	43.555	2.412	.047
	DGL 2000	1.261	4	.315	.577	.679
	DGL 2001	25.331	4	6.333	1.804	.126
	delta DGL	28.451	4	7.113	2.269	.060
	Seedling Volume 2000	8.872	4	2.218	1.237	.293
	Seedling Volume 2001	1602.825	4	400.706	2.469	.043
	Absolute Growth Rate	1511.707	4	377.927	2.478	.042
	Relative Growth Rate	3.492	4	.873	2.314	.056
	Seedling Vigor	3.614	4	.903	2.383	.050
Error	Height 2000	20646.951	1344	15.362		

	Height 2001	46718.203	1344	34.761		
	delta Height	24267.598	1344	18.056		
	DGL 2000	734.056	1344	.546		
	DGL 2001	4716.978	1344	3.510		
	delta DGL	4213.590	1344	3.135		
	Seedling Volume 2000	2410.666	1344	1.794		
	Seedling Volume 2001	218168.174	1344	162.328		
	Absolute Growth Rate	204965.598	1344	152.504		
	Relative Growth Rate	506.973	1344	.377		
	Seedling Vigor	509.493	1344	.379		
Total	Height 2000	472141.250	1425			
	Height 2001	965629.050	1425			
	delta Height	114623.480	1425			
	DGL 2000	21765.640	1425			
	DGL 2001	75632.760	1425			
	delta DGL	20462.460	1425			
	Seedling Volume 2000	14222.175	1425			
	Seedling Volume 2001	661139.054	1425			
	Absolute Growth Rate	531402.365	1425			
	Relative Growth Rate	3837.794	1425			
	Seedling Vigor	7517.000	1425			
Corrected Total	Height 2000	31510.827	1424			
	Height 2001	71836.238	1424			
	delta Height	35321.442	1424			
	DGL 2000	966.122	1424			
	DGL 2001	8675.691	1424			
	delta DGL	7342.989	1424			
	Seedling Volume 2000	3309.667	1424			
	Seedling Volume 2001	343968.051	1424			
	Absolute Growth Rate	320981.055	1424			
	Relative Growth Rate	830.412	1424			
	Seedling Vigor	584.755	1424			

Will Lake: Seedling Harvest

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	# roots top	632.348(a)	35	18.067	1.710	.012
	# roots middle	2278.486(b)	35	65.100	2.214	.000
	# roots bottom	18992.551(c)	35	542.644	1.668	.016
	% roots top	2634.207(d)	35	75.263	1.307	.131
	% roots middle	8867.895(e)	35	253.368	2.400	.000
	% roots bottom	12665.674(f)	35	361.876	2.537	.000
	total # roots	22154.768(g)	35	632.993	1.502	.045
	root dry mass	897.763(h)	35	25.650	3.649	.000
	shoot dry mass	5542.473(i)	35	158.356	3.078	.000
	Root to Shoot Ratio	3.403(j)	35	.097	.573	.974
	Seedling dry mass	10476.885(k)	35	299.340	4.795	.000
Intercept	# roots top	2298.364	1	2298.364	217.592	.000
	# roots middle	12803.311	1	12803.311	435.430	.000
	# roots bottom	135101.546	1	135101.546	415.288	.000
	% roots top	11058.037	1	11058.037	191.986	.000
	% roots middle	57176.244	1	57176.244	541.607	.000
	% roots bottom	492507.583	1	492507.583	3452.966	.000
	total # roots	279475.688	1	279475.688	663.310	.000
	root dry mass	2109.280	1	2109.280	300.082	.000
	shoot dry mass	12684.805	1	12684.805	246.535	.000
	Root to Shoot Ratio	29.833	1	29.833	175.667	.000
	Seedling dry mass	25139.619	1	25139.619	402.698	.000
SOILTRT	# roots top	25.398	2	12.699	1.202	.303
	# roots middle	67.488	2	33.744	1.148	.320
	# roots bottom	1144.873	2	572.436	1.760	.175
	% roots top	6.015	2	3.008	.052	.949
	% roots middle	516.289	2	258.144	2.445	.089
	% roots bottom	612.497	2	306.248	2.147	.120
	total # roots	1280.164	2	640.082	1.519	.221
	root dry mass	124.953	2	62.476	8.888	.000
	shoot dry mass	1100.587	2	550.294	10.695	.000
	Root to Shoot Ratio	.099	2	.049	.291	.747
	Seedling dry mass	1960.302	2	980.151	15.701	.000
CONT	# roots top	33.531	2	16.765	1.587	.207
	# roots middle	150.818	2	75.409	2.565	.080
	# roots bottom	1110.286	2	555.143	1.706	.184
	% roots top	40.943	2	20.472	.355	.701
	% roots middle	484.483	2	242.242	2.295	.103
	% roots bottom	750.052	2	375.026	2.629	.075
	total # roots	581.986	2	290.993	.691	.502
	root dry mass	47.853	2	23.926	3.404	.035
	shoot dry mass	92.420	2	46.210	.898	.409

	Root to Shoot Ratio	.707	2	.353	2.081	.128
	Seedling dry mass	262.153	2	131.077	2.100	.125
INOC	# roots top	13.460	2	6.730	.637	.530
	# roots middle	236.501	2	118.250	4.022	.019
	# roots bottom	250.643	2	125.321	.385	.681
	% roots top	34.513	2	17.256	.300	.741
	% roots middle	631.839	2	315.920	2.993	.052
	% roots bottom	454.289	2	227.144	1.593	.206
	total # roots	326.995	2	163.497	.388	.679
	root dry mass	7.007	2	3.503	.498	.608
	shoot dry mass	64.637	2	32.319	.628	.535
	Root to Shoot Ratio	.051	2	.025	.149	.861
	Seedling dry mass	112.426	2	56.213	.900	.408
SOILTRT * CONT	# roots top	82.550	4	20.638	1.954	.103
	# roots middle	48.743	4	12.186	.414	.798
	# roots bottom	1321.050	4	330.262	1.015	.401
	% roots top	800.718	4	200.180	3.475	.009
	% roots middle	277.923	4	69.481	.658	.622
	% roots bottom	921.008	4	230.252	1.614	.172
	total # roots	1296.152	4	324.038	.769	.547
	root dry mass	7.888	4	1.972	.281	.890
	shoot dry mass	138.501	4	34.625	.673	.611
	Root to Shoot Ratio	.204	4	.051	.300	.878
	Seedling dry mass	162.841	4	40.710	.652	.626
SOILTRT * INOC	# roots top	94.306	4	23.577	2.232	.067
	# roots middle	102.996	4	25.749	.876	.479
	# roots bottom	3143.618	4	785.904	2.416	.050
	% roots top	462.989	4	115.747	2.010	.095
	% roots middle	784.890	4	196.222	1.859	.119
	% roots bottom	890.233	4	222.558	1.560	.186
	total # roots	4613.552	4	1153.388	2.737	.030
	root dry mass	47.973	4	11.993	1.706	.150
	shoot dry mass	342.568	4	85.642	1.664	.160
	Root to Shoot Ratio	.149	4	.037	.219	.927
	Seedling dry mass	642.414	4	160.603	2.573	.039
CONT * INOC	# roots top	127.630	4	31.907	3.021	.019
	# roots middle	70.617	4	17.654	.600	.663
	# roots bottom	1952.296	4	488.074	1.500	.204
	% roots top	547.825	4	136.956	2.378	.053
	% roots middle	321.821	4	80.455	.762	.551
	% roots bottom	1041.024	4	260.256	1.825	.126
	total # roots	1779.914	4	444.978	1.056	.379
	root dry mass	13.709	4	3.427	.488	.745
	shoot dry mass	52.530	4	13.132	.255	.906
	Root to Shoot Ratio	.203	4	.051	.300	.878
	Seedling dry mass	90.044	4	22.511	.361	.836

Error	# roots top	2091.417	198	10.563			
	# roots middle	5821.958	198	29.404			
	# roots bottom	64413.333	198	325.320			
	% roots top	11404.408	198	57.598			
	% roots middle	20902.430	198	105.568			
	% roots bottom	28241.373	198	142.633			
	total # roots	83424.292	198	421.335			
	root dry mass	1391.742	198	7.029			
	shoot dry mass	10187.547	198	51.452			
	Root to Shoot Ratio	33.625	198	.170			
	Seedling dry mass	12360.738	198	62.428			
Total	# roots top	8405.000	234				
	# roots middle	32552.000	234				
	# roots bottom	362753.000	234				
	% roots top	40280.000	234				
	% roots middle	137661.800	234				
	% roots bottom	1120829.660	234				
	total # roots	683600.000	234				
	root dry mass	6988.263	234				
	shoot dry mass	44230.782	234				
	Root to Shoot Ratio	98.290	234				
	Seedling dry mass	79182.472	234				
Corrected Total	# roots top	2723.765	233				
	# roots middle	8100.444	233				
	# roots bottom	83405.885	233				
	% roots top	14038.615	233				
	% roots middle	29770.325	233				
	% roots bottom	40907.046	233				
	total # roots	105579.060	233				
	root dry mass	2289.505	233				
	shoot dry mass	15730.020	233				
	Root to Shoot Ratio	37.028	233				
	Seedling dry mass	22837.623	233				

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Bulk Density	3221382.929(a)	23	140060.127	4.671	.000
	% Sand	4048.182(b)	23	176.008	4.431	.000
	% Silt	4073.781(c)	23	177.121	4.581	.000
	% Clay	1289.147(d)	23	56.050	2.309	.014
	pH	11.566(e)	23	.503	9.256	.000
	Moisture Factor	.004(f)	23	.000	10.923	.000
	Total C	101.768(g)	23	4.425	3.390	.001
	Total N	.096(h)	23	.004	4.407	.000
	Mineral N	11958.164(i)	23	519.920	6.212	.000
	Available P	16349.853(j)	23	710.863	3.134	.002
	Exch K	3.300(k)	23	.143	1.629	.100
	CEC	3415.561(l)	23	148.503	9.733	.000
	Exch Al	.382(m)	23	.017	.776	.734
	Exch Ca	716.171(n)	23	31.138	5.178	.000
	Exch Mg	1237.105(o)	23	53.787	13.688	.000
	Exch Mn	.885(p)	23	.038	3.311	.001
	Exch Na	.740(q)	23	.032	11.439	.000
	s(ave) May	5461863.710(r)	23	237472.335	3.933	.000
	m(ave) May	829.185(s)	23	36.052	5.803	.000
	s(ave) June	24500875.900(t)	23	1065255.474	2.321	.014
	m(ave) June	2620.964(u)	23	113.955	4.537	.000
Intercept	Bulk Density	57756632.510	1	57756632.510	1926.142	.000
	% Sand	143062.510	1	143062.510	3601.696	.000
	% Silt	61559.923	1	61559.923	1592.017	.000
	% Clay	7485.897	1	7485.897	308.392	.000
	pH	2015.363	1	2015.363	37096.482	.000
	Moisture Factor	46.412	1	46.412	2668814.105	.000
	Total C	406.661	1	406.661	311.526	.000
	Total N	.529	1	.529	557.460	.000
	Mineral N	18192.047	1	18192.047	217.346	.000
	Available P	128112.765	1	128112.765	564.807	.000
	Exch K	21.157	1	21.157	240.187	.000
	CEC	42188.415	1	42188.415	2765.034	.000
	Exch Al	.061	1	.061	2.865	.100
	Exch Ca	14680.633	1	14680.633	2441.174	.000
	Exch Mg	5994.306	1	5994.306	1525.414	.000
	Exch Mn	.660	1	.660	56.798	.000
	Exch Na	1.315	1	1.315	467.770	.000
	s(ave) May	56316907.523	1	56316907.523	932.741	.000
	m(ave) May	65575.383	1	65575.383	10554.853	.000
	s(ave) June	155332832.261	1	155332832.261	338.472	.000

	m(ave) June	40690.074	1	40690.074	1620.130	.000
TREAT	Bulk Density	1382902.034	3	460967.345	15.373	.000
	% Sand	1071.698	3	357.233	8.994	.000
	% Silt	2085.527	3	695.176	17.978	.000
	% Clay	789.343	3	263.114	10.839	.000
	pH	6.492	3	2.164	39.833	.000
	Moisture Factor	.003	3	.001	51.324	.000
	Total C	29.492	3	9.831	7.531	.001
	Total N	.024	3	.008	8.606	.000
	Mineral N	3658.486	3	1219.495	14.570	.000
	Available P	5877.166	3	1959.055	8.637	.000
	Exch K	1.291	3	.430	4.887	.007
	CEC	2397.834	3	799.278	52.385	.000
	Exch Al	.095	3	.032	1.482	.238
	Exch Ca	465.398	3	155.133	25.796	.000
	Exch Mg	764.464	3	254.821	64.846	.000
	Exch Mn	.140	3	.047	4.010	.016
	Exch Na	.311	3	.104	36.823	.000
	s(ave) May	3309808.605	3	1103269.535	18.273	.000
	m(ave) May	336.741	3	112.247	18.067	.000
	s(ave) June	6350797.145	3	2116932.382	4.613	.009
	m(ave) June	1272.567	3	424.189	16.890	.000
DEPTH	Bulk Density	738140.480	1	738140.480	24.616	.000
	% Sand	3.438	1	3.438	.087	.771
	% Silt	4.629	1	4.629	.120	.732
	% Clay	15.984	1	15.984	.659	.423
	pH	.419	1	.419	7.707	.009
	Moisture Factor	.000	1	.000	10.198	.003
	Total C	30.586	1	30.586	23.431	.000
	Total N	.026	1	.026	27.415	.000
	Mineral N	899.494	1	899.494	10.747	.003
	Available P	395.694	1	395.694	1.744	.196
	Exch K	.114	1	.114	1.292	.264
	CEC	175.016	1	175.016	11.471	.002
	Exch Al	.013	1	.013	.619	.437
	Exch Ca	31.277	1	31.277	5.201	.029
	Exch Mg	68.485	1	68.485	17.428	.000
	Exch Mn	.089	1	.089	7.652	.009
	Exch Na	.012	1	.012	4.197	.049
	s(ave) May	230994.809	1	230994.809	3.826	.059
	m(ave) May	6.251	1	6.251	1.006	.323
	s(ave) June	104571.268	1	104571.268	.228	.636
	m(ave) June	.589	1	.589	.023	.879
TREAT * DEPTH	Bulk Density	153055.088	3	51018.363	1.701	.186
	% Sand	12.688	3	4.229	.106	.956
	% Silt	40.163	3	13.388	.346	.792
	% Clay	18.170	3	6.057	.250	.861

	pH	.516	3	.172	3.165	.038
	Moisture Factor	.000	3	5.507E-05	3.167	.038
	Total C	2.631	3	.877	.672	.576
	Total N	.006	3	.002	2.244	.102
	Mineral N	3013.985	3	1004.662	12.003	.000
	Available P	733.775	3	244.592	1.078	.372
	Exch K	.206	3	.069	.778	.515
	CEC	68.111	3	22.704	1.488	.236
	Exch Al	.038	3	.013	.589	.626
	Exch Ca	17.399	3	5.800	.964	.421
	Exch Mg	20.494	3	6.831	1.738	.179
	Exch Mn	.166	3	.055	4.748	.008
	Exch Na	.002	3	.001	.206	.892
	s(ave) May	338882.478	3	112960.826	1.871	.154
	m(ave) May	.146	3	.049	.008	.999
	s(ave) June	3086875.169	3	1028958.390	2.242	.102
	m(ave) June	23.020	3	7.673	.306	.821
Error	Bulk Density	959541.000	32	29985.656		
	% Sand	1271.068	32	39.721		
	% Silt	1237.372	32	38.668		
	% Clay	776.767	32	24.274		
	pH	1.738	32	.054		
	Moisture Factor	.001	32	1.739E-05		
	Total C	41.772	32	1.305		
	Total N	.030	32	.001		
	Mineral N	2678.430	32	83.701		
	Available P	7258.427	32	226.826		
	Exch K	2.819	32	.088		
	CEC	488.251	32	15.258		
	Exch Al	.685	32	.021		
	Exch Ca	192.440	32	6.014		
	Exch Mg	125.748	32	3.930		
	Exch Mn	.372	32	.012		
	Exch Na	.090	32	.003		
	s(ave) May	1932092.066	32	60377.877		
	m(ave) May	198.810	32	6.213		
	s(ave) June	14685567.358	32	458923.980		
	m(ave) June	803.690	32	25.115		
Total	Bulk Density	63768616.000	56			
	% Sand	163994.909	56			
	% Silt	73958.822	56			
	% Clay	9801.707	56			
	pH	2202.554	56			
	Moisture Factor	51.203	56			
	Total C	632.297	56			
	Total N	.745	56			
	Mineral N	36948.680	56			

	Available P	172402.200	56			
	Exch K	29.735	56			
	CEC	48571.585	56			
	Exch Al	1.156	56			
	Exch Ca	16394.334	56			
	Exch Mg	7701.314	56			
	Exch Mn	2.138	56			
	Exch Na	2.242	56			
	s(ave) May	68795031.166	56			
	m(ave) May	73304.306	56			
	s(ave) June	206442568.439	56			
	m(ave) June	47412.694	56			
Corrected Total	Bulk Density	4180923.929	55			
	% Sand	5319.250	55			
	% Silt	5311.153	55			
	% Clay	2065.914	55			
	pH	13.304	55			
	Moisture Factor	.005	55			
	Total C	143.540	55			
	Total N	.126	55			
	Mineral N	14636.594	55			
	Available P	23608.279	55			
	Exch K	6.118	55			
	CEC	3903.811	55			
	Exch Al	1.067	55			
	Exch Ca	908.612	55			
	Exch Mg	1362.854	55			
	Exch Mn	1.257	55			
	Exch Na	.830	55			
	s(ave) May	7393955.776	55			
	m(ave) May	1027.996	55			
	s(ave) June	39186443.258	55			
	m(ave) June	3424.654	55			

Will Lake: Morphotype

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	# Non Mycorrhizal	339215.795(a)	35	9691.880	4.601	.000
	% colonization	80667.096(b)	35	2304.774	4.800	.000
	richness	512.500(c)	35	14.643	5.220	.000
	diversity	210.991(d)	35	6.028	3.484	.000
	evenness	71.517(e)	35	2.043	2.773	.000
Intercept	# Non Mycorrhizal	2593503.150	1	2593503.150	1231.240	.000
	% colonization	193485.268	1	193485.268	402.944	.000
	richness	1076.737	1	1076.737	383.857	.000
	diversity	284.231	1	284.231	164.275	.000
	evenness	64.178	1	64.178	87.104	.000
LANDTRT	# Non Mycorrhizal	41469.114	2	20734.557	9.844	.000
	% colonization	9085.689	2	4542.844	9.461	.000
	richness	52.880	2	26.440	9.426	.000
	diversity	46.628	2	23.314	13.475	.000
	evenness	7.937	2	3.968	5.386	.005
CONT	# Non Mycorrhizal	4090.039	2	2045.019	.971	.381
	% colonization	1032.351	2	516.176	1.075	.344
	richness	43.858	2	21.929	7.818	.001
	diversity	3.674	2	1.837	1.062	.348
	evenness	.736	2	.368	.499	.608
INOC	# Non Mycorrhizal	16129.873	2	8064.937	3.829	.024
	% colonization	4415.509	2	2207.754	4.598	.012
	richness	13.805	2	6.902	2.461	.089
	diversity	1.331	2	.665	.385	.681
	evenness	5.940	2	2.970	4.031	.020
LANDTRT * CONT	# Non Mycorrhizal	23964.037	4	5991.009	2.844	.026
	% colonization	4847.823	4	1211.956	2.524	.043
	richness	13.209	4	3.302	1.177	.323
	diversity	3.171	4	.793	.458	.766
	evenness	8.163	4	2.041	2.770	.029
LANDTRT * INOC	# Non Mycorrhizal	37455.709	4	9363.927	4.445	.002
	% colonization	9048.488	4	2262.122	4.711	.001
	richness	32.682	4	8.170	2.913	.023
	diversity	5.812	4	1.453	.840	.502
	evenness	5.284	4	1.321	1.793	.133
CONT * INOC	# Non Mycorrhizal	92360.815	4	23090.204	10.962	.000
	% colonization	21650.554	4	5412.639	11.272	.000
	richness	21.750	4	5.438	1.938	.107
	diversity	59.769	4	14.942	8.636	.000
	evenness	8.474	4	2.119	2.875	.025
Error	# Non Mycorrhizal	320175.200	152	2106.416		

	% colonization	72987.231	152	480.179		
	richness	426.367	152	2.805		
	diversity	262.992	152	1.730		
	evenness	111.993	152	.737		
Total	# Non Mycorrhizal	3691897.000	188			
	% colonization	453494.736	188			
	richness	2139.000	188			
	diversity	907.781	188			
	evenness	286.850	188			
Corrected Total	# Non Mycorrhizal	659390.995	187			
	% colonization	153654.327	187			
	richness	938.867	187			
	diversity	473.983	187			
	evenness	183.510	187			

Will Lake: Morphotype Relative Abundance

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	non-mycorrhizal	8.067(a)	35	.230	4.800	.000
	incomplete	.919(b)	35	.026	2.973	.000
	MRA	.527(c)	35	.015	1.694	.016
	Thelophora	.019(d)	35	.001	.931	.583
	E-Strain 2	.240(e)	35	.007	1.043	.415
	Tomentella 2	.015(f)	35	.000	1.275	.161
	Rhizopogon 1	.079(g)	35	.002	1.714	.014
	Cenococcum	.021(h)	35	.001	1.133	.297
	Hebeloma 1 (+cl)	1.615(i)	35	.046	1.774	.010
	Hebeloma 2 (-cl)	.507(j)	35	.014	1.735	.012
	Laccaria	.035(k)	35	.001	1.382	.095
	E-Strain 1	.647(l)	35	.018	2.652	.000
	Suillus	.346(m)	35	.010	2.012	.002
	Hebeloma + MRA	.103(n)	35	.003	1.594	.029
	Hebeloma 3 (-eh)	.225(o)	35	.006	1.173	.253
	Thelophora 2 (-cl)	.003(p)	35	9.234E-05	.964	.533
	Rhizopogon 2	.004(q)	35	.000	.920	.601
	Tuber	.006(r)	35	.000	.848	.710
	Suillus 2	.533(s)	35	.015	3.561	.000
	Tomentella 1	.011(t)	35	.000	1.057	.396
	E-Strain 2 + MRA	.006(u)	35	.000	1.307	.138
	E-Strain 2 + Suillus 2	.003(e)	35	7.885E-05	1.043	.416
Intercept	non-mycorrhizal	58.143	1	58.143	1210.867	.000
	incomplete	.319	1	.319	36.155	.000
	MRA	.406	1	.406	45.708	.000
	Thelophora	.002	1	.002	3.534	.062
	E-Strain 2	.077	1	.077	11.668	.001
	Tomentella 2	4.059E-06	1	4.059E-06	.012	.913
	Rhizopogon 1	.007	1	.007	5.612	.019
	Cenococcum	.003	1	.003	5.108	.025
	Hebeloma 1 (+cl)	1.458	1	1.458	56.057	.000
	Hebeloma 2 (-cl)	.046	1	.046	5.565	.020
	Laccaria	.002	1	.002	3.385	.068
	E-Strain 1	.112	1	.112	16.075	.000
	Suillus	.071	1	.071	14.391	.000
	Hebeloma + MRA	.021	1	.021	11.498	.001
	Hebeloma 3 (-eh)	.049	1	.049	8.946	.003
	Thelophora 2 (-cl)	.000	1	.000	1.995	.160
	Rhizopogon 2	.000	1	.000	3.286	.072
	Tuber	.000	1	.000	1.018	.315
	Suillus 2	.034	1	.034	7.883	.006
	Tomentella 1	.001	1	.001	3.064	.082

	E-Strain 2 + MRA	.000	1	.000	1.404	.238
	E-Strain 2 + Suillus 2	.000	1	.000	3.668	.057
LANDTRT	non-mycorrhizal	.909	2	.454	9.461	.000
	incomplete	.019	2	.010	1.097	.337
	MRA	.065	2	.032	3.638	.029
	Thelophora	.000	2	.000	.232	.793
	E-Strain 2	.015	2	.008	1.177	.311
	Tomentella 2	8.105E-06	2	4.053E-06	.012	.988
	Rhizopogon 1	.000	2	.000	.148	.862
	Cenococcum	.001	2	.001	1.126	.327
	Hebeloma 1 (+cl)	.458	2	.229	8.800	.000
	Hebeloma 2 (-cl)	.015	2	.007	.873	.420
	Laccaria	.000	2	6.144E-05	.085	.918
	E-Strain 1	.048	2	.024	3.414	.035
	Suillus	.030	2	.015	3.098	.048
	Hebeloma + MRA	.031	2	.016	8.425	.000
	Hebeloma 3 (-eh)	.015	2	.007	1.341	.265
	Thelophora 2 (-cl)	.000	2	.000	2.015	.137
	Rhizopogon 2	.000	2	.000	.857	.426
	Tuber	.000	2	.000	1.028	.360
	Suillus 2	.017	2	.009	2.011	.137
	Tomentella 1	.002	2	.001	3.094	.048
	E-Strain 2 + MRA	.000	2	.000	1.149	.320
	E-Strain 2 + Suillus 2	.001	2	.000	3.639	.029
CONT	non-mycorrhizal	.103	2	.052	1.075	.344
	incomplete	.002	2	.001	.119	.888
	MRA	.022	2	.011	1.234	.294
	Thelophora	.001	2	.001	1.193	.306
	E-Strain 2	7.873E-05	2	3.937E-05	.006	.994
	Tomentella 2	.001	2	.000	1.224	.297
	Rhizopogon 1	.008	2	.004	2.877	.059
	Cenococcum	.001	2	.001	1.400	.250
	Hebeloma 1 (+cl)	.058	2	.029	1.121	.329
	Hebeloma 2 (-cl)	.002	2	.001	.090	.914
	Laccaria	.003	2	.001	2.033	.135
	E-Strain 1	.028	2	.014	2.045	.133
	Suillus	.006	2	.003	.599	.551
	Hebeloma + MRA	.001	2	.000	.202	.817
	Hebeloma 3 (-eh)	.002	2	.001	.149	.862
	Thelophora 2 (-cl)	7.896E-05	2	3.948E-05	.412	.663
	Rhizopogon 2	.000	2	.000	.966	.383
	Tuber	.000	2	9.005E-05	.432	.650
	Suillus 2	.004	2	.002	.509	.602
	Tomentella 1	.000	2	.000	.000	1.000
	E-Strain 2 + MRA	.000	2	8.442E-05	.694	.501
	E-Strain 2 + Suillus 2	.000	2	5.768E-05	.763	.468
INOC	non-mycorrhizal	.442	2	.221	4.598	.012

	incomplete	.106	2	.053	5.975	.003
	MRA	.113	2	.056	6.335	.002
	Thelophora	.001	2	.001	1.079	.343
	E-Strain 2	.005	2	.003	.400	.671
	Tomentella 2	.000	2	.000	.475	.623
	Rhizopogon 1	.003	2	.001	1.033	.359
	Cenococcum	.002	2	.001	1.685	.189
	Hebeloma 1 (+cl)	.013	2	.007	.258	.773
	Hebeloma 2 (-cl)	.064	2	.032	3.854	.023
	Laccaria	.000	2	.000	.175	.839
	E-Strain 1	.040	2	.020	2.871	.060
	Suillus	.001	2	.001	.150	.860
	Hebeloma + MRA	.003	2	.001	.732	.482
	Hebeloma 3 (-eh)	.034	2	.017	3.087	.049
	Thelophora 2 (-cl)	.000	2	.000	1.429	.243
	Rhizopogon 2	1.626E-05	2	8.129E-06	.061	.941
	Tuber	.000	2	8.943E-05	.429	.652
	Suillus 2	.019	2	.009	2.176	.117
	Tomentella 1	.001	2	.000	1.500	.226
	E-Strain 2 + MRA	.000	2	.000	2.018	.136
	E-Strain 2 + Suillus 2	1.463E-05	2	7.315E-06	.097	.908
LANDTRT * CONT	non-mycorrhizal	.485	4	.121	2.524	.043
	incomplete	.104	4	.026	2.940	.022
	MRA	.067	4	.017	1.897	.114
	Thelophora	.003	4	.001	1.116	.351
	E-Strain 2	.013	4	.003	.498	.738
	Tomentella 2	.002	4	.000	1.231	.300
	Rhizopogon 1	.017	4	.004	3.201	.015
	Cenococcum	.002	4	.000	.886	.474
	Hebeloma 1 (+cl)	.180	4	.045	1.728	.147
	Hebeloma 2 (-cl)	.045	4	.011	1.362	.250
	Laccaria	.004	4	.001	1.494	.207
	E-Strain 1	.021	4	.005	.771	.546
	Suillus	.031	4	.008	1.562	.187
	Hebeloma + MRA	.002	4	.001	.289	.885
	Hebeloma 3 (-eh)	.036	4	.009	1.649	.165
	Thelophora 2 (-cl)	.000	4	3.985E-05	.416	.797
	Rhizopogon 2	.001	4	.000	1.124	.347
	Tuber	.000	4	9.099E-05	.436	.782
	Suillus 2	.057	4	.014	3.328	.012
	Tomentella 1	.000	4	.000	.000	1.000
	E-Strain 2 + MRA	.001	4	.000	2.319	.060
	E-Strain 2 + Suillus 2	.000	4	5.668E-05	.749	.560
LANDTRT * INOC	non-mycorrhizal	.905	4	.226	4.711	.001
	incomplete	.114	4	.028	3.224	.014
	MRA	.022	4	.005	.611	.655

		Thelophora	.004	4	.001	1.880	.117
		E-Strain 2	.052	4	.013	1.967	.102
		Tomentella 2	.001	4	.000	.475	.754
		Rhizopogon 1	.008	4	.002	1.567	.186
		Cenococcum	.003	4	.001	1.412	.233
		Hebeloma 1 (+cl)	.213	4	.053	2.045	.091
		Hebeloma 2 (-cl)	.028	4	.007	.833	.506
		Laccaria	.005	4	.001	1.650	.165
		E-Strain 1	.053	4	.013	1.917	.110
		Suillus	.084	4	.021	4.284	.003
		Hebeloma + MRA	.010	4	.003	1.371	.246
		Hebeloma 3 (-eh)	.011	4	.003	.496	.738
		Thelophora 2 (-cl)	.001	4	.000	1.455	.219
		Rhizopogon 2	.000	4	6.194E-05	.463	.763
		Tuber	.000	4	9.068E-05	.435	.783
		Suillus 2	.065	4	.016	3.794	.006
		Tomentella 1	.002	4	.000	1.520	.199
		E-Strain 2 + MRA	.000	4	9.716E-05	.799	.528
		E-Strain 2 + Suillus 2	2.873E-05	4	7.184E-06	.095	.984
	CONT * INOC	non-mycorrhizal	2.165	4	.541	11.272	.000
		incomplete	.060	4	.015	1.707	.151
		MRA	.091	4	.023	2.558	.041
		Thelophora	.003	4	.001	1.141	.340
		E-Strain 2	.020	4	.005	.762	.552
		Tomentella 2	.002	4	.001	1.495	.207
		Rhizopogon 1	.007	4	.002	1.325	.263
		Cenococcum	.003	4	.001	1.191	.317
		Hebeloma 1 (+cl)	.042	4	.011	.404	.805
		Hebeloma 2 (-cl)	.073	4	.018	2.197	.072
		Laccaria	.003	4	.001	.997	.411
		E-Strain 1	.150	4	.037	5.366	.000
		Suillus	.032	4	.008	1.609	.175
		Hebeloma + MRA	.009	4	.002	1.213	.308
		Hebeloma 3 (-eh)	.041	4	.010	1.883	.116
		Thelophora 2 (-cl)	.001	4	.000	1.320	.265
		Rhizopogon 2	.000	4	5.345E-05	.400	.809
		Tuber	.000	4	3.649E-05	.175	.951
		Suillus 2	.115	4	.029	6.745	.000
		Tomentella 1	.000	4	.000	.000	1.000
		E-Strain 2 + MRA	.000	4	.000	.988	.416
		E-Strain 2 + Suillus 2	.000	4	.000	.000	1.000
	Error	non-mycorrhizal	7.299	152	.048		
		incomplete	1.343	152	.009		
		MRA	1.350	152	.009		
		Thelophora	.090	152	.001		
		E-Strain 2	1.000	152	.007		
		Tomentella 2	.051	152	.000		

	Rhizopogon 1	.200	152	.001			
	Cenococcum	.081	152	.001			
	Hebeloma 1 (+cl)	3.954	152	.026			
	Hebeloma 2 (-cl)	1.268	152	.008			
	Laccaria	.110	152	.001			
	E-Strain 1	1.059	152	.007			
	Suillus	.746	152	.005			
	Hebeloma + MRA	.280	152	.002			
	Hebeloma 3 (-eh)	.835	152	.005			
	Thelophora 2 (-cl)	.015	152	9.581E-05			
	Rhizopogon 2	.020	152	.000			
	Tuber	.032	152	.000			
	Suillus 2	.650	152	.004			
	Tomentella 1	.046	152	.000			
	E-Strain 2 + MRA	.018	152	.000			
	E-Strain 2 + Suillus 2	.011	152	7.563E-05			
Total	non-mycorrhizal	83.190	188				
	incomplete	2.894	188				
	MRA	2.453	188				
	Thelophora	.112	188				
	E-Strain 2	1.380	188				
	Tomentella 2	.066	188				
	Rhizopogon 1	.298	188				
	Cenococcum	.108	188				
	Hebeloma 1 (+cl)	7.080	188				
	Hebeloma 2 (-cl)	1.902	188				
	Laccaria	.152	188				
	E-Strain 1	1.937	188				
	Suillus	1.212	188				
	Hebeloma + MRA	.404	188				
	Hebeloma 3 (-eh)	1.114	188				
	Thelophora 2 (-cl)	.018	188				
	Rhizopogon 2	.025	188				
	Tuber	.038	188				
	Suillus 2	1.267	188				
	Tomentella 1	.057	188				
	E-Strain 2 + MRA	.024	188				
	E-Strain 2 + Suillus 2	.014	188				
Corrected Total	non-mycorrhizal	15.365	187				
	incomplete	2.263	187				
	MRA	1.877	187				
	Thelophora	.109	187				
	E-Strain 2	1.240	187				
	Tomentella 2	.066	187				
	Rhizopogon 1	.279	187				
	Cenococcum	.102	187				
	Hebeloma 1 (+cl)	5.569	187				

	Hebeloma 2 (-cl)	1.775	187			
	Laccaria	.145	187			
	E-Strain 1	1.706	187			
	Suillus	1.092	187			
	Hebeloma + MRA	.383	187			
	Hebeloma 3 (-eh)	1.060	187			
	Thelophora 2 (-cl)	.018	187			
	Rhizopogon 2	.025	187			
	Tuber	.038	187			
	Suillus 2	1.182	187			
	Tomentella 1	.057	187			
	E-Strain 2 + MRA	.024	187			
	E-Strain 2 + Suillus 2	.014	187			

Appendix II

This appendix contains the results of the analysis of variance to accompany Chapter 3. Tables have been abbreviated to exclude site effects, and multi-way interactions.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Seedling Height	150.284(b)	8	18.786	2.102	.042
	Seedling Diameter	2.527(c)	8	.316	1.318	.243
	Initial Volume	5.131(d)	8	.641	1.520	.160
Intercept	Seedling Height	28815.267	1	28815.267	3224.790	.000
	Seedling Diameter	889.241	1	889.241	3711.027	.000
	Initial Volume	218.453	1	218.453	517.886	.000
CONT	Seedling Height	11.912	2	5.956	.667	.516
	Seedling Diameter	.344	2	.172	.718	.490
	Initial Volume	.147	2	7.367E-02	.175	.840
INOC	Seedling Height	122.524	2	61.262	6.856	.002
	Seedling Diameter	.889	2	.444	1.855	.162
	Initial Volume	3.043	2	1.522	3.607	.031
CONT * INOC	Seedling Height	15.849	4	3.962	.443	.777
	Seedling Diameter	1.294	4	.323	1.350	.257
	Initial Volume	1.940	4	.485	1.150	.338
Error	Seedling Height	884.619	99	8.936		
	Seedling Diameter	23.723	99	.240		
	Initial Volume	41.760	99	.422		
Total	Seedling Height	29850.170	108			
	Seedling Diameter	915.490	108			
	Initial Volume	265.344	108			
Corrected Total	Seedling Height	1034.903	107			
	Seedling Diameter	26.249	107			
	Initial Volume	46.891	107			

Graham River: Root Emergence at Lifting

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Top Root Plug	1358.361(a)	8	169.795	2.484	.021
	Middle Root Plug	1454.861(b)	8	181.858	2.184	.041
	Bottom Root Plug	8225.028(c)	8	1028.128	3.317	.003
	Total Emergent Roots	14579.444(d)	8	1822.431	2.286	.032
	% Top Root Plug	1888.838(e)	8	236.105	5.946	.000
	% Middle Root Plug	995.820(f)	8	124.478	2.651	.014
	% Bottom Root Plug	3206.146(g)	8	400.768	4.421	.000
Intercept	Top Root Plug	16501.389	1	16501.389	241.414	.000
	Middle Root Plug	33325.014	1	33325.014	400.272	.000
	Bottom Root Plug	141423.347	1	141423.347	456.283	.000
	Total Emergent Roots	472068.056	1	472068.056	592.147	.000
	% Top Root Plug	25757.690	1	25757.690	648.702	.000
	% Middle Root Plug	51530.130	1	51530.130	1097.298	.000
	% Bottom Root Plug	212559.607	1	212559.607	2344.755	.000
CONT	Top Root Plug	440.444	2	220.222	3.222	.047
	Middle Root Plug	378.528	2	189.264	2.273	.111
	Bottom Root Plug	3173.861	2	1586.931	5.120	.009
	Total Emergent Roots	2992.861	2	1496.431	1.877	.161
	% Top Root Plug	1288.572	2	644.286	16.226	.000
	% Middle Root Plug	22.320	2	11.160	.238	.789
	% Bottom Root Plug	1192.415	2	596.208	6.577	.003
INOC	Top Root Plug	238.194	2	119.097	1.742	.183
	Middle Root Plug	423.444	2	211.722	2.543	.087
	Bottom Root Plug	370.861	2	185.431	.598	.553
	Total Emergent Roots	1218.028	2	609.014	.764	.470
	% Top Root Plug	303.038	2	151.519	3.816	.027
	% Middle Root Plug	386.615	2	193.308	4.116	.021
	% Bottom Root Plug	802.394	2	401.197	4.426	.016
CONT * INOC	Top Root Plug	679.722	4	169.931	2.486	.052
	Middle Root Plug	652.889	4	163.222	1.960	.111
	Bottom Root Plug	4680.306	4	1170.076	3.775	.008
	Total Emergent Roots	10368.556	4	2592.139	3.251	.017
	% Top Root Plug	297.228	4	74.307	1.871	.126
	% Middle Root Plug	586.885	4	146.721	3.124	.021
	% Bottom Root Plug	1211.337	4	302.834	3.341	.015
Error	Top Root Plug	4306.250	63	68.353		
	Middle Root Plug	5245.125	63	83.256		
	Bottom Root Plug	19526.625	63	309.946		
	Total Emergent Roots	50224.500	63	797.214		
	% Top Root Plug	2501.509	63	39.706		
	% Middle Root Plug	2958.538	63	46.961		
	% Bottom Root Plug	5711.153	63	90.653		

Total	Top Root Plug	22166.000	72			
	Middle Root Plug	40025.000	72			
	Bottom Root Plug	169175.000	72			
	Total Emergent Roots	536872.000	72			
	% Top Root Plug	30148.037	72			
	% Middle Root Plug	-55484.489	72			
	% Bottom Root Plug	221476.905	72			
Corrected Total	Top Root Plug	5664.611	71			
	Middle Root Plug	6699.986	71			
	Bottom Root Plug	27751.653	71			
	Total Emergent Roots	64803.944	71			
	% Top Root Plug	4390.347	71			
	% Middle Root Plug	3954.359	71			
	% Bottom Root Plug	8917.299	71			

Graham River: % Colonization at Lifting

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	39590.727(a)	8	4948.841	7.783	.000
Intercept	323007.162	1	323007.162	507.964	.000
CONT	36826.788	2	18413.394	28.957	.000
INOC	746.886	2	373.443	.587	.558
CONT * INOC	2017.052	4	504.263	.793	.533
Error	51506.723	81	635.885		
Total	414104.612	90			
Corrected Total	91097.450	89			

Graham River: Soil Mineral Suite

Source		Sum of Squares	df	Mean Square	F	Sig.
Available P (ppm)	Between Groups	282.724	2	141.362	.662	.534
	Within Groups	2563.440	12	213.620		
	Total	2846.164	14			
CEC (Ba) CMOL+/Kg	Between Groups	.438	2	.219	.085	.919
	Within Groups	30.815	12	2.568		
	Total	31.253	14			
Exch Al CMOL+/Kg	Between Groups	43.665	2	21.833	9.954	.003
	Within Groups	26.320	12	2.193		
	Total	69.985	14			
Exch Ca CMOL+/Kg	Between Groups	23.533	2	11.766	3.884	.050
	Within Groups	36.355	12	3.030		
	Total	59.888	14			
Exch Fe CMOL+/Kg	Between Groups	.109	2	.055	2.431	.130
	Within Groups	.270	12	.022		
	Total	.379	14			
Exch K CMOL+/Kg	Between Groups	.004	2	.002	1.571	.248
	Within Groups	.015	12	.001		
	Total	.019	14			
Exch Mg CMOL+/Kg	Between Groups	2.189	2	1.094	3.883	.050
	Within Groups	3.383	12	.282		
	Total	5.572	14			
Exch Mn CMOL+/Kg	Between Groups	.001	2	.000	2.401	.133
	Within Groups	.002	12	.000		
	Total	.003	14			
Exch Na CMOL+/Kg	Between Groups	.000	2	.000	1.140	.352
	Within Groups	.001	12	.000		
	Total	.001	14			
Minrl N ppm	Between Groups	10.929	2	5.465	.969	.407
	Within Groups	67.680	12	5.640		
	Total	78.609	14			
pH/H20	Between Groups	1.523	2	.761	4.747	.030
	Within Groups	1.925	12	.160		
	Total	3.448	14			
Total C (%)	Between Groups	2.452	2	1.226	6.413	.013
	Within Groups	2.294	12	.191		
	Total	4.746	14			
Total N (%)	Between Groups	.001	2	.001	2.563	.118
	Within Groups	.003	12	.000		
	Total	.004	14			
Moisture Factor	Between Groups	.000	2	.000	4.462	.036
	Within Groups	.000	12	.000		
	Total	.000	14			

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Diameter 2000	22.855(a)	53	.431	2.611	.000
	Diameter 2001	65.459(b)	53	1.235	2.365	.000
	delta Diameter	37.964(c)	53	.716	1.963	.000
	Height 2000	3599.010(d)	53	67.906	7.744	.000
	Height 2001	3209.353(e)	53	60.554	3.521	.000
	delta Height	1156.147(f)	53	21.814	1.701	.002
	Volume 2000	80.018(g)	53	1.510	4.812	.000
	Volume 2001	725.268(h)	53	13.684	3.209	.000
	delta Volume	427.462(i)	53	8.065	2.521	.000
	Seedling Vigour	17.935(j)	53	.338	1.362	.046
Intercept	Diameter 2000	8926.930	1	8926.930	54049.901	.000
	Diameter 2001	23533.684	1	23533.684	45063.634	.000
	delta Diameter	3472.096	1	3472.096	9513.178	.000
	Height 2000	303356.101	1	303356.101	34592.786	.000
	Height 2001	501422.452	1	501422.452	29155.885	.000
	delta Height	24754.041	1	24754.041	1929.869	.000
	Volume 2000	2337.619	1	2337.619	7450.873	.000
	Volume 2001	27332.591	1	27332.591	6410.139	.000
	delta Volume	13683.751	1	13683.751	4277.938	.000
	Seedling Vigour	3068.497	1	3068.497	12350.539	.000
TREAT	Diameter 2000	2.878E-02	1	2.878E-02	.174	.676
	Diameter 2001	2.391	1	2.391	4.578	.033
	delta Diameter	1.895	1	1.895	5.193	.023
	Height 2000	7.965	1	7.965	.908	.341
	Height 2001	132.208	1	132.208	7.687	.006
	delta Height	75.271	1	75.271	5.868	.016
	Volume 2000	.361	1	.361	1.152	.283
	Volume 2001	29.231	1	29.231	6.855	.009
	delta Volume	23.091	1	23.091	7.219	.007
	Seedling Vigour	.548	1	.548	2.206	.138
CONT	Diameter 2000	7.344	2	3.672	22.232	.000
	Diameter 2001	3.984	2	1.992	3.814	.022
	delta Diameter	.840	2	.420	1.151	.317
	Height 2000	1906.289	2	953.144	108.690	.000
	Height 2001	1068.365	2	534.182	31.061	.000
	delta Height	176.035	2	88.017	6.862	.001
	Volume 2000	36.140	2	18.070	57.596	.000
	Volume 2001	137.739	2	68.870	16.152	.000
	delta Volume	32.799	2	16.400	5.127	.006
	Seedling Vigour	.428	2	.214	.861	.423
INOC	Diameter 2000	2.047	2	1.024	6.197	.002

	Diameter 2001	5.570	2	2.785	5.332	.005
	delta Diameter	.959	2	.480	1.314	.269
	Height 2000	333.601	2	166.800	19.021	.000
	Height 2001	308.871	2	154.436	8.980	.000
	delta Height	3.245	2	1.622	.126	.881
	Volume 2000	8.605	2	4.302	13.713	.000
	Volume 2001	89.021	2	44.510	10.439	.000
	delta Volume	43.227	2	21.614	6.757	.001
	Seedling Vigour	.409	2	.204	.823	.439
TREAT * CONT	Diameter 2000	6.523E-02	2	3.261E-02	.197	.821
	Diameter 2001	.227	2	.114	.218	.804
	delta Diameter	9.697E-02	2	4.848E-02	.133	.876
	Height 2000	98.909	2	49.455	5.639	.004
	Height 2001	5.919	2	2.960	.172	.842
	delta Height	62.912	2	31.456	2.452	.087
	Volume 2000	.846	2	.423	1.348	.260
	Volume 2001	1.111	2	.555	.130	.878
	delta Volume	1.095	2	.547	.171	.843
	Seedling Vigour	.329	2	.165	.662	.516
TREAT * INOC	Diameter 2000	.278	2	.139	.843	.431
	Diameter 2001	.631	2	.316	.604	.547
	delta Diameter	8.373E-02	2	4.187E-02	.115	.892
	Height 2000	16.299	2	8.149	.929	.395
	Height 2001	17.955	2	8.977	.522	.593
	delta Height	4.917	2	2.458	.192	.826
	Volume 2000	5.005E-02	2	2.503E-02	.080	.923
	Volume 2001	4.074	2	2.037	.478	.620
	delta Volume	3.779	2	1.890	.591	.554
	Seedling Vigour	.133	2	6.642E-02	.267	.765
CONT * INOC	Diameter 2000	1.220	4	.305	1.846	.118
	Diameter 2001	3.465	4	.866	1.659	.157
	delta Diameter	2.727	4	.682	1.868	.114
	Height 2000	109.695	4	27.424	3.127	.014
	Height 2001	151.767	4	37.942	2.206	.066
	delta Height	12.570	4	3.142	.245	.913
	Volume 2000	2.121	4	.530	1.690	.150
	Volume 2001	24.443	4	6.111	1.433	.221
	delta Volume	16.908	4	4.227	1.321	.260
	Seedling Vigour	.858	4	.214	.863	.485
Error	Diameter 2000	167.308	1013	.165		
	Diameter 2001	529.021	1013	.522		
	delta Diameter	369.722	1013	.365		
	Height 2000	8883.347	1013	8.769		
	Height 2001	17421.558	1013	17.198		
	delta Height	12993.545	1013	12.827		
	Volume 2000	317.816	1013	.314		
	Volume 2001	4319.394	1013	4.264		

	delta Volume	3240.262	1013	3.199		
	Seedling Vigour	251.680	1013	.248		
Total	Diameter 2000	9122.500	1067			
	Diameter 2001	24133.500	1067			
	delta Diameter	3878.460	1067			
	Height 2000	315908.080	1067			
	Height 2001	521955.780	1067			
	delta Height	38862.180	1067			
	Volume 2000	2734.286	1067			
	Volume 2001	32334.909	1067			
	delta Volume	17324.334	1067			
	Seedling Vigour	3340.000	1067			
Corrected Total	Diameter 2000	190.163	1066			
	Diameter 2001	594.480	1066			
	delta Diameter	407.686	1066			
	Height 2000	12482.357	1066			
	Height 2001	20630.911	1066			
	delta Height	14149.692	1066			
	Volume 2000	397.834	1066			
	Volume 2001	5044.662	1066			
	delta Volume	3667.724	1066			
	Seedling Vigour	269.616	1066			

Graham River: Harvest

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Top of Plug	836.924(a)	52	16.095	1.798	.001
	Middle of Plug	1338.598(b)	52	25.742	1.441	.030
	Bottom of Plug	3225.254(c)	52	62.024	1.010	.459
	Total # of Roots	8273.901(d)	52	159.113	1.373	.052
	% of Total - Top	6931.213(e)	52	133.293	1.512	.017
	% of Total - Middle	5948.896(f)	52	114.402	.894	.683
	% of Total - Bottom	12836.177(g)	52	246.850	1.309	.084
	Shoot Dry Weight	203.657(h)	52	3.916	1.941	.000
	Root Dry Weight	53.670(i)	52	1.032	1.768	.002
	Seedling Dry Weight	398.108(j)	52	7.656	3.058	.000
	Root:Shoot	610.730(k)	52	11.745	.875	.717
Intercept	Top of Plug	14888.519	1	14888.519	1663.195	.000
	Middle of Plug	30783.186	1	30783.186	1722.720	.000
	Bottom of Plug	82328.184	1	82328.184	1341.116	.000
	Total # of Roots	341521.931	1	341521.931	2947.849	.000
	% of Total - Top	196396.702	1	196396.702	2227.928	.000
	% of Total - Middle	386623.863	1	386623.863	3019.779	.000
	% of Total - Bottom	931226.038	1	931226.038	4936.647	.000
	Shoot Dry Weight	5883.790	1	5883.790	2916.493	.000
	Root Dry Weight	919.202	1	919.202	1574.214	.000
	Seedling Dry Weight	11454.615	1	11454.615	4575.654	.000
	Root:Shoot	5078.107	1	5078.107	378.218	.000
TREAT	Top of Plug	27.346	1	27.346	3.055	.081
	Middle of Plug	41.778	1	41.778	2.338	.127
	Bottom of Plug	319.932	1	319.932	5.212	.023
	Total # of Roots	874.949	1	874.949	7.552	.006
	% of Total - Top	3.636	1	3.636	.041	.839
	% of Total - Middle	351.439	1	351.439	2.745	.098
	% of Total - Bottom	428.607	1	428.607	2.272	.133
	Shoot Dry Weight	1.101	1	1.101	.546	.460
	Root Dry Weight	.146	1	.146	.250	.618
	Seedling Dry Weight	.446	1	.446	.178	.673
	Root:Shoot	22.937	1	22.937	1.708	.192
CONT	Top of Plug	40.190	2	20.095	2.245	.107
	Middle of Plug	110.893	2	55.447	3.103	.046
	Bottom of Plug	389.286	2	194.643	3.171	.043
	Total # of Roots	1158.101	2	579.051	4.998	.007
	% of Total - Top	246.934	2	123.467	1.401	.248
	% of Total - Middle	181.536	2	90.768	.709	.493
	% of Total - Bottom	732.119	2	366.060	1.941	.145
	Shoot Dry Weight	30.412	2	15.206	7.537	.001
	Root Dry Weight	4.363	2	2.182	3.736	.025

	Seedling Dry Weight	57.815	2	28.907	11.547	.000
	Root:Shoot	7.094	2	3.547	.264	.768
INOC	Top of Plug	1.653	2	.826	.092	.912
	Middle of Plug	70.082	2	35.041	1.961	.142
	Bottom of Plug	30.851	2	15.425	.251	.778
	Total # of Roots	133.797	2	66.898	.577	.562
	% of Total - Top	176.190	2	88.095	.999	.369
	% of Total - Middle	351.037	2	175.519	1.371	.255
	% of Total - Bottom	93.633	2	46.816	.248	.780
	Shoot Dry Weight	11.742	2	5.871	2.910	.056
	Root Dry Weight	.345	2	.172	.295	.744
	Seedling Dry Weight	15.855	2	7.928	3.167	.043
	Root:Shoot	25.332	2	12.666	.943	.390
TREAT * CONT	Top of Plug	31.630	2	15.815	1.767	.172
	Middle of Plug	70.434	2	35.217	1.971	.141
	Bottom of Plug	100.942	2	50.471	.822	.440
	Total # of Roots	23.552	2	11.776	.102	.903
	% of Total - Top	300.416	2	150.208	1.704	.183
	% of Total - Middle	558.652	2	279.326	2.182	.114
	% of Total - Bottom	1609.916	2	804.958	4.267	.015
	Shoot Dry Weight	2.855	2	1.427	.707	.494
	Root Dry Weight	2.099	2	1.050	1.798	.167
	Seedling Dry Weight	9.320	2	4.660	1.861	.157
	Root:Shoot	46.695	2	23.348	1.739	.177
TREAT * INOC	Top of Plug	39.457	2	19.728	2.204	.112
	Middle of Plug	29.666	2	14.833	.830	.437
	Bottom of Plug	116.222	2	58.111	.947	.389
	Total # of Roots	504.397	2	252.198	2.177	.115
	% of Total - Top	112.330	2	56.165	.637	.529
	% of Total - Middle	48.351	2	24.176	.189	.828
	% of Total - Bottom	98.073	2	49.037	.260	.771
	Shoot Dry Weight	4.341	2	2.170	1.076	.342
	Root Dry Weight	3.099	2	1.549	2.654	.072
	Seedling Dry Weight	14.766	2	7.383	2.949	.054
	Root:Shoot	99.793	2	49.896	3.716	.025
CONT * INOC	Top of Plug	8.923	4	2.231	.249	.910
	Middle of Plug	225.318	4	56.329	3.152	.014
	Bottom of Plug	61.709	4	15.427	.251	.909
	Total # of Roots	550.695	4	137.674	1.188	.315
	% of Total - Top	423.791	4	105.948	1.202	.310
	% of Total - Middle	709.606	4	177.402	1.386	.238
	% of Total - Bottom	494.210	4	123.552	.655	.624
	Shoot Dry Weight	8.090	4	2.022	1.002	.406
	Root Dry Weight	1.396	4	.349	.598	.664
	Seedling Dry Weight	9.547	4	2.387	.953	.433
	Root:Shoot	10.614	4	2.653	.198	.940
Error	Top of Plug	3330.055	372	8.952		

	Middle of Plug	6647.247	372	17.869		
	Bottom of Plug	22836.276	372	61.388		
	Total # of Roots	43097.921	372	115.855		
	% of Total - Top	32792.608	372	88.152		
	% of Total - Middle	47627.358	372	128.031		
	% of Total - Bottom	70172.340	372	188.635		
	Shoot Dry Weight	750.480	372	2.017		
	Root Dry Weight	217.215	372	.584		
	Seedling Dry Weight	931.259	372	2.503		
	Root:Shoot	4994.618	372	13.426		
Total	Top of Plug	19431.000	425			
	Middle of Plug	39833.000	425			
	Bottom of Plug	110063.000	425			
	Total # of Roots	401641.000	425			
	% of Total - Top	242289.850	425			
	% of Total - Middle	457019.340	425			
	% of Total - Bottom	1036014.870	425			
	Shoot Dry Weight	7011.842	425			
	Root Dry Weight	1211.690	425			
	Seedling Dry Weight	13102.889	425			
	Root:Shoot	10847.289	425			
Corrected Total	Top of Plug	4166.979	424			
	Middle of Plug	7985.845	424			
	Bottom of Plug	26061.529	424			
	Total # of Roots	51371.821	424			
	% of Total - Top	39723.821	424			
	% of Total - Middle	53576.254	424			
	% of Total - Bottom	83008.517	424			
	Shoot Dry Weight	954.137	424			
	Root Dry Weight	270.885	424			
	Seedling Dry Weight	1329.366	424			
	Root:Shoot	5605.348	424			

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Relative Growth Rate	24.971(a)	53	.471	2.381	.000
	Absolute Growth Rate	427.450(b)	53	8.065	2.521	.000
Intercept	Relative Growth Rate	1566.053	1	1566.053	7915.793	.000
	Absolute Growth Rate	13683.593	1	13683.593	4277.884	.000
SITE	Relative Growth Rate	2.381	2	1.190	6.016	.003
	Absolute Growth Rate	72.950	2	36.475	11.403	.000
TREAT	Relative Growth Rate	1.333	1	1.333	6.738	.010
	Absolute Growth Rate	23.090	1	23.090	7.219	.007
CONT	Relative Growth Rate	6.608	2	3.304	16.700	.000
	Absolute Growth Rate	32.797	2	16.399	5.127	.006
INOC	Relative Growth Rate	.303	2	.151	.766	.465
	Absolute Growth Rate	43.220	2	21.610	6.756	.001
TREAT * CONT	Relative Growth Rate	.517	2	.258	1.306	.271
	Absolute Growth Rate	1.095	2	.547	.171	.843
TREAT * INOC	Relative Growth Rate	7.740E-02	2	3.870E-02	.196	.822
	Absolute Growth Rate	3.779	2	1.890	.591	.554
CONT * INOC	Relative Growth Rate	.856	4	.214	1.082	.364
	Absolute Growth Rate	16.911	4	4.228	1.322	.260
Error	Relative Growth Rate	200.411	1013	.198		
	Absolute Growth Rate	3240.266	1013	3.199		
Total	Relative Growth Rate	1791.030	1067			
	Absolute Growth Rate	17324.169	1067			
Corrected Total	Relative Growth Rate	225.381	1066			
	Absolute Growth Rate	3667.715	1066			

Graham River: Morphotype

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	% Colonization	35149.631(a)	52	675.954	1.404	.071
	Richness	188.549(b)	52	3.626	2.204	.000
	Richness/incomplete	290.790(c)	52	5.592	2.605	.000
	Simpson's 1/D	123.187(d)	52	2.369	3.040	.000
	Simpson's E	2.844(e)	52	5.470E-02	2.026	.001
	Shannon's H'	33.146(f)	52	.637	3.634	.000
	Shannon's E	14.097(g)	52	.271	3.705	.000
Intercept	% Colonization	373219.485	1	373219.485	775.043	.000
	Richness	1035.127	1	1035.127	629.157	.000
	Richness/incomplete	1503.392	1	1503.392	700.298	.000
	Simpson's 1/D	745.015	1	745.015	956.000	.000
	Simpson's E	91.489	1	91.489	3388.448	.000
	Shannon's H'	88.489	1	88.489	504.478	.000
	Shannon's E	50.460	1	50.460	689.740	.000
TREAT	% Colonization	3120.284	1	3120.284	6.480	.012
	Richness	2.019	1	2.019	1.227	.270
	Richness/incomplete	.450	1	.450	.210	.648
	Simpson's 1/D	3.772E-03	1	3.772E-03	.005	.945
	Simpson's E	1.598E-03	1	1.598E-03	.059	.808
	Shannon's H'	3.440E-04	1	3.440E-04	.002	.965
	Shannon's E	1.046E-02	1	1.046E-02	.143	.706
CONT	% Colonization	3762.892	2	1881.446	3.907	.023
	Richness	17.339	2	8.670	5.269	.007
	Richness/incomplete	20.806	2	10.403	4.846	.010
	Simpson's 1/D	5.422	2	2.711	3.479	.034
	Simpson's E	.249	2	.125	4.616	.012
	Shannon's H'	2.101	2	1.051	5.990	.003
	Shannon's E	.983	2	.492	6.719	.002
INOC	% Colonization	625.271	2	312.635	.649	.524
	Richness	12.897	2	6.448	3.919	.023
	Richness/incomplete	19.879	2	9.940	4.630	.012
	Simpson's 1/D	5.947	2	2.974	3.816	.025
	Simpson's E	.111	2	5.573E-02	2.064	.132
	Shannon's H'	1.707	2	.853	4.864	.009
	Shannon's E	.392	2	.196	2.679	.073
TREAT * CONT	% Colonization	698.669	2	349.335	.725	.486
	Richness	8.828	2	4.414	2.683	.073
	Richness/incomplete	12.372	2	6.186	2.881	.060
	Simpson's 1/D	7.054	2	3.527	4.526	.013
	Simpson's E	1.352E-02	2	6.759E-03	.250	.779
	Shannon's H'	1.509	2	.754	4.300	.016
	Shannon's E	.403	2	.202	2.756	.068

TREAT * INOC	% Colonization	293.522	2	146.761	.305	.738
	Richness	.850	2	.425	.258	.773
	Richness/incomplete	1.727	2	.864	.402	.670
	Simpson's 1/D	.671	2	.336	.431	.651
	Simpson's E	.237	2	.119	4.394	.015
	Shannon's H'	4.747E-02	2	2.374E-02	.135	.874
	Shannon's E	.270	2	.135	1.844	.163
CONT * INOC	% Colonization	122.658	4	30.664	.064	.992
	Richness	18.902	4	4.725	2.872	.026
	Richness/incomplete	26.815	4	6.704	3.123	.018
	Simpson's 1/D	10.086	4	2.521	3.235	.015
	Simpson's E	.216	4	5.393E-02	1.997	.100
	Shannon's H'	3.104	4	.776	4.424	.002
	Shannon's E	1.515	4	.379	5.176	.001
Error	% Colonization	52488.608	109	481.547		
	Richness	179.333	109	1.645		
	Richness/incomplete	234.000	109	2.147		
	Simpson's 1/D	84.944	109	.779		
	Simpson's E	2.943	109	2.700E-02		
	Shannon's H'	19.119	109	.175		
	Shannon's E	7.974	109	7.316E-02		
Total	% Colonization	473858.149	162			
	Richness	1431.000	162			
	Richness/incomplete	2068.000	162			
	Simpson's 1/D	967.919	162			
	Simpson's E	99.547	162			
	Shannon's H'	141.545	162			
	Shannon's E	72.215	162			
Corrected Total	% Colonization	87638.239	161			
	Richness	367.883	161			
	Richness/incomplete	524.790	161			
	Simpson's 1/D	208.131	161			
	Simpson's E	5.788	161			
	Shannon's H'	52.265	161			
	Shannon's E	22.071	161			

Graham River: Relative Abundance

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Incomplete	4529.157(a)	52	87.099	1.370	.086
	Cenococcum	1617.664(b)	52	31.109	5.422	.000
	Hebeloma/no clamps	33383.770(c)	52	641.996	2.744	.000
	MRA	5739.277(d)	52	110.371	1.273	.147
	Suillus	11.885(e)	52	.229	1.099	.335
	Hebeloma/with clamps	23920.118(f)	52	460.002	1.934	.002
	Hebeloma / MRA	3514.908(g)	52	67.594	2.501	.000
	Rhizopogon	467.441(h)	52	8.989	2.110	.001
	E Strain	342.038(i)	52	6.578	2.664	.000
	Hebeloma / no hyphae	14695.821(j)	52	282.612	1.363	.090
	Laccaria	.519(k)	52	9.988E-03	1.029	.442
	Piloderma	129.866(l)	52	2.497	3.846	.000
	Amphinema	1558.860(m)	52	29.978	8.460	.000
	Tuber	92.668(k)	52	1.782	1.029	.442
	Non Mycorrhizal	34215.119(n)	52	657.983	1.395	.074
Intercept	Incomplete	4839.311	1	4839.311	76.098	.000
	Cenococcum	367.216	1	367.216	64.008	.000
	Hebeloma/no clamps	8259.974	1	8259.974	35.303	.000
	MRA	5297.074	1	5297.074	61.087	.000
	Suillus	.859	1	.859	4.130	.045
	Hebeloma/with clamps	30779.471	1	30779.471	129.435	.000
	Hebeloma / MRA	1476.334	1	1476.334	54.635	.000
	Rhizopogon	13.204	1	13.204	3.099	.081
	E Strain	32.982	1	32.982	13.360	.000
	Hebeloma / no hyphae	14291.439	1	14291.439	68.908	.000
	Laccaria	9.209E-03	1	9.209E-03	.948	.332
	Piloderma	3.882	1	3.882	5.978	.016
	Amphinema	131.422	1	131.422	37.088	.000
	Tuber	1.643	1	1.643	.948	.332
	Non Mycorrhizal	418656.435	1	418656.435	887.542	.000
TREAT	Incomplete	83.060	1	83.060	1.306	.256
	Cenococcum	45.429	1	45.429	7.919	.006
	Hebeloma/no clamps	1665.123	1	1665.123	7.117	.009
	MRA	402.491	1	402.491	4.642	.033
	Suillus	.391	1	.391	1.881	.173
	Hebeloma/with clamps	1152.993	1	1152.993	4.849	.030
	Hebeloma / MRA	43.728	1	43.728	1.618	.206
	Rhizopogon	12.910	1	12.910	3.030	.085
	E Strain	7.565	1	7.565	3.064	.083
	Hebeloma / no hyphae	713.898	1	713.898	3.442	.066
	Laccaria	1.005E-02	1	1.005E-02	1.035	.311
	Piloderma	6.793	1	6.793	10.460	.002

	Amphinema	.116	1	.116	.033	.857
	Tuber	1.794	1	1.794	1.035	.311
	Non Mycorrhizal	2972.460	1	2972.460	6.302	.014
CONT	Incomplete	54.112	2	27.056	.425	.655
	Cenococcum	41.403	2	20.701	3.608	.030
	Hebeloma/no clamps	145.602	2	72.801	.311	.733
	MRA	35.541	2	17.771	.205	.815
	Suillus	.237	2	.119	.570	.567
	Hebeloma/with clamps	1399.091	2	699.545	2.942	.057
	Hebeloma / MRA	215.124	2	107.562	3.981	.021
	Rhizopogon	6.465	2	3.232	.759	.471
	E Strain	41.578	2	20.789	8.421	.000
	Hebeloma / no hyphae	206.625	2	103.313	.498	.609
	Laccaria	1.983E-02	2	9.914E-03	1.021	.364
	Piloderma	1.941	2	.970	1.494	.229
	Amphinema	92.999	2	46.499	13.122	.000
	Tuber	3.538	2	1.769	1.021	.364
	Non Mycorrhizal	3801.245	2	1900.623	4.029	.021
INOC	Incomplete	113.225	2	56.612	.890	.414
	Cenococcum	5.870	2	2.935	.512	.601
	Hebeloma/no clamps	2355.504	2	1177.752	5.034	.008
	MRA	218.382	2	109.191	1.259	.288
	Suillus	7.507E-02	2	3.753E-02	.180	.835
	Hebeloma/with clamps	308.131	2	154.066	.648	.525
	Hebeloma / MRA	143.794	2	71.897	2.661	.074
	Rhizopogon	39.932	2	19.966	4.686	.011
	E Strain	4.142	2	2.071	.839	.435
	Hebeloma / no hyphae	473.862	2	236.931	1.142	.323
	Laccaria	1.988E-02	2	9.941E-03	1.024	.363
	Piloderma	1.946	2	.973	1.498	.228
	Amphinema	115.286	2	57.643	16.267	.000
	Tuber	3.547	2	1.774	1.024	.363
	Non Mycorrhizal	544.116	2	272.058	.577	.563
TREAT * CONT	Incomplete	83.116	2	41.558	.653	.522
	Cenococcum	20.350	2	10.175	1.774	.175
	Hebeloma/no clamps	592.949	2	296.474	1.267	.286
	MRA	670.290	2	335.145	3.865	.024
	Suillus	2.537E-02	2	1.268E-02	.061	.941
	Hebeloma/with clamps	108.028	2	54.014	.227	.797
	Hebeloma / MRA	124.690	2	62.345	2.307	.104
	Rhizopogon	6.365	2	3.182	.747	.476
	E Strain	27.560	2	13.780	5.582	.005
	Hebeloma / no hyphae	64.563	2	32.281	.156	.856
	Laccaria	1.819E-02	2	9.097E-03	.937	.395
	Piloderma	4.107	2	2.054	3.162	.046
	Amphinema	3.836	2	1.918	.541	.584
	Tuber	3.246	2	1.623	.937	.395

	Non Mycorrhizal	618.229	2	309.114	.655	.521
TREAT * INOC	Incomplete	20.145	2	10.072	.158	.854
	Cenococcum	64.182	2	32.091	5.594	.005
	Hebeloma/no clamps	629.512	2	314.756	1.345	.265
	MRA	125.957	2	62.978	.726	.486
	Suillus	.154	2	7.717E-02	.371	.691
	Hebeloma/with clamps	45.930	2	22.965	.097	.908
	Hebeloma / MRA	124.371	2	62.186	2.301	.105
	Rhizopogon	39.400	2	19.700	4.624	.012
	E Strain	17.714	2	8.857	3.588	.031
	Hebeloma / no hyphae	85.983	2	42.991	.207	.813
	Laccaria	1.830E-02	2	9.150E-03	.942	.393
	Piloderma	4.051	2	2.025	3.119	.048
	Amphinema	56.172	2	28.086	7.926	.001
	Tuber	3.265	2	1.632	.942	.393
	Non Mycorrhizal	315.908	2	157.954	.335	.716
CONT * INOC	Incomplete	462.706	4	115.676	1.819	.130
	Cenococcum	150.404	4	37.601	6.554	.000
	Hebeloma/no clamps	4907.310	4	1226.827	5.244	.001
	MRA	316.261	4	79.065	.912	.460
	Suillus	.917	4	.229	1.102	.359
	Hebeloma/with clamps	4014.970	4	1003.743	4.221	.003
	Hebeloma / MRA	120.852	4	30.213	1.118	.352
	Rhizopogon	26.323	4	6.581	1.544	.194
	E Strain	14.983	4	3.746	1.517	.202
	Hebeloma / no hyphae	1411.305	4	352.826	1.701	.155
	Laccaria	3.838E-02	4	9.595E-03	.988	.417
	Piloderma	8.730	4	2.183	3.361	.012
	Amphinema	80.059	4	20.015	5.648	.000
	Tuber	6.847	4	1.712	.988	.417
	Non Mycorrhizal	110.073	4	27.518	.058	.994
Error	Incomplete	6931.683	109	63.593		
	Cenococcum	625.335	109	5.737		
	Hebeloma/no clamps	25502.804	109	233.971		
	MRA	9451.712	109	86.713		
	Suillus	22.667	109	.208		
	Hebeloma/with clamps	25919.989	109	237.798		
	Hebeloma / MRA	2945.376	109	27.022		
	Rhizopogon	464.430	109	4.261		
	E Strain	269.091	109	2.469		
	Hebeloma / no hyphae	22606.498	109	207.399		
	Laccaria	1.058	109	9.710E-03		
	Piloderma	70.786	109	.649		
	Amphinema	386.241	109	3.543		
	Tuber	188.833	109	1.732		
	Non Mycorrhizal	51415.639	109	471.703		
Total	Incomplete	16096.295	162			

	Cenococcum	2651.057	162			
	Hebeloma/no clamps	67913.774	162			
	MRA	20593.790	162			
	Suillus	35.333	162			
	Hebeloma/with clamps	81760.049	162			
	Hebeloma / MRA	8022.006	162			
	Rhizopogon	949.002	162			
	E Strain	640.825	162			
	Hebeloma / no hyphae	51758.364	162			
	Laccaria	1.588	162			
	Piloderma	205.578	162			
	Amphinema	2092.524	162			
	Tuber	283.249	162			
	Non Mycorrhizal	511580.900	162			
Corrected Total	Incomplete	11460.841	161			
	Cenococcum	2242.998	161			
	Hebeloma/no clamps	58886.573	161			
	MRA	15190.989	161			
	Suillus	34.552	161			
	Hebeloma/with clamps	49840.107	161			
	Hebeloma / MRA	6460.284	161			
	Rhizopogon	931.871	161			
	E Strain	611.129	161			
	Hebeloma / no hyphae	37302.319	161			
	Laccaria	1.578	161			
	Piloderma	200.652	161			
	Amphinema	1945.100	161			
	Tuber	281.500	161			
	Non Mycorrhizal	85630.757	161			

Appendix III

Ectomycorrhizal Morphological Types

This appendix contains complete descriptions of the ectomycorrhizal morphological types encountered on seedling root systems throughout the two studies presented in this thesis. Classification of morphological types follows the taxonomy outlined by the United States National Center for Biotechnology Information (Domarachev *et al.* 2003). Ectomycorrhizae were classified into morphological types using the methods of Goodman *et al.* (Goodman *et al.* 1996; Durall *et al.* 1999; Hagerman *et al.* 1999) and compared to descriptions published in Agerer (1987-2000) and Ingleby *et al.* (1990).

Literature Cited

Agerer, R. Colour Atlas of Ectomycorrhizae. 1987-2000. Einhorn-Verlag Eduard Dietenberger. Schwäbisch Gmüng, Germany.

Domarachev, M., Federhen, S., Hotton, C., Leipe, D., Soussov, V., Sternberg, R., and Turner, S. 2003. Taxonomy Browser [online]. United States National Center for Biotechnology Information. Available from http://www.ncbi.nlm.nih.gov/Taxonomy/ Browser/wwwtax.cgi [updated June 24, 2003, cited October 14, 2003].

Durall, D.M., Jones, M.D., Wright, E.F., Kroeger, P., and Coates, K.D. 1999. Species richness of ectomycorrhizal fungi in cutblocks of different sizes in the interior cedar-hemlock forests of northwestern British Columbia: sorocarps and ectomycorrhizae. Can. J. For. Res. 29: 1322-1332.

Goodman, D.M., Durall, D.M., Trofymow, J.A., and Berch, S.M. 1996.A manual of concise descriptions of North American ectomycorrhizae. Describing ectomycorrhizae. Mycologue Publications. Sidney, B.C.

Hagerman, S.M., Jones, M.D., Bradfield, G.E., Gillespie, M., and Durall, D.M. Effects of clear-cut logging on the diversity and persistance of ectomycorrhizae at a subalpine forest. Can. J. For. Res. 29, 124-134. 1999.

Ingleby, K., Mason, P.A., Last, F.T., and Fleming, L.V. 1990. Identification of Ectomycorrhizae. Her Majesty's Stationary Office, London, England.

Morphological Type: *Amphinema* – like

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Stereales
Family: Atheliaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: ESSF mv2

Distinguishing Features: bright yellow to orange tips with abundant cottony hyphae and strands

Abundant hyphae and strands Mantle 1000x

Morphology of Ectomycorrhizal System: non-branched or monopodial pinnate system, tips yellow to orange 3-6 mm, cottony shiny reflective tips with abundant emanating hyphae and common mycelial strands

Morphology of Mycelial Strands: common, loose undifferentiated, 2-3 mm diameter, cell width 2-4 μm clear no ornamentation, septa and clamps common, protruding hyphae hemispherical with distinctive dichotomous branching

Morphology of Emanating Hyphae: abundant pale yellow, cell width 2-4 μm clear no ornamentation, septa and clamps common. H-shaped anastamoses common, distinctive dichotomous branching hemispherical hyphae

Anatomy of Mantle in Plan View: thick loose hemispherical felt prosenchyma, cell width 2-4 µm, clear no ornamentation, abundant hyphal junctions septa and clamps common, H-shaped anastamoses common

Other Features: cystidia absent

Morphological Type: *Cenococcum geophilum* – like

Phylum: Ascomycota
Class: Dothideomycetes
Order: no rank (mitosporic Dothideomycete)
Family:

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: dark brown to black thick mantle with distinct mantle pattern visible at 200x

Cenococcum – like root tip Mantle 400x

Morphology of Ectomycorrhizal System: non-branched system, tips are straight, clubbed shape, black coarsely grainy, reflective and shiny, 2-5 mm

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: common, straight, black and wiry, very coarse

Anatomy of Mantle in Plan View: thick mantle, net synenchyma, distinct arrangement of cells, thick walled, ~ 4 x 10 μm, septa common, fungus completely obscures host

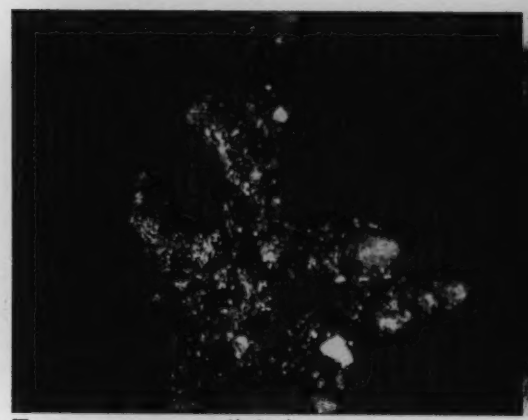
Other Features: cystidia absent

Morphological Type: E-strain I (*Wilcoxina* – like)

Phylum: Ascomycota
Class: Pezizomycetes
Order: Pezizales
Family: Pyronemataceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: tortuous bent tips with distinctive verrucose hyphae



Tortuous monopodial pinnate system

Mantle 1000x

Morphology of Ectomycorrhizal System: monopodial pinnate branching and single non-branched, tips tortuous or slightly bent, tips brown to dark-brown smooth and matte, pale brown-orange tip apices

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: rare to abundant, brown 5-10 μm wide, straight with verrucose ornamentation

Anatomy of Mantle in Plan View: thin net synenchyma, inflated cells often with constricted septa, 3-4 μm wide various lengths, no ornamentation or cellular contents, septa common, no clamps

Other Features: cystidia absent

Morphological Type: E-strain II (*Wilcoxina* – like)

Phylum: Ascomycota
Class: Pezizomycetes
Order: Pezizales
Family: Pyronemataceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: straight tips with bulbous apices lacking hyphae

Tortuous root tips Mantle 1000x

Morphology of Ectomycorrhizal System: monopodial pinnate branching and single non-branched, tips tortuous or slightly bent, tips brown to dark-brown smooth and matte, pale brown-orange tip apices

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: none

Anatomy of Mantle in Plan View: thin net synenchyma, inflated cells often with constricted septa, 3-4 μm wide various lengths, no ornamentation or cellular contents, septa common, no clamps

Other Features: cystidia absent

Morphological Type: *Hebeloma* – like I

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Agaricales
Family: Cortinariaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: non-branched, tips straight or slightly bent, cottony hyphae with abundant clamps

Root Tips Emanating hyphae with clamps 400x

Morphology of Ectomycorrhizal System: not branched, tips slightly bent or straight, smooth finely grainy shiny, young tips pale, older tips light orange-brown

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: not branched, tips bent or straight, smooth finely grainy, young tips pale older tips light orange-brown

Anatomy of Mantle in Plan View: net synenchyma, cells ~ 4μm diameter, septa common, clear contents

Other Features: cystidia absent

Morphological Type: *Hebeloma* – like II

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Agaricales
Family: Cortinariaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: non-branched, tips slightly bent, cottony like emanating hyphae without clamps

Hebeloma – like II root tips Mantle 400x

Morphology of Ectomycorrhizal System: not branched, tips bent or straight, smooth finely grainy, young tips pale older tips light orange-brown

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: clear hyphae, rare to common, 3-5 μm diameter, lack clamps, septa rare to common

Anatomy of Mantle in Plan View: thin net synenchyma, cells ~ 4μm diameter, septa common clear contents

Other Features: cystidia absent

Morphological Type: *Hebeloma* – like III

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Agaricales
Family: Cortinariaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: dichotomous branched or straight system, light yellowish-brown smooth reflective tips

Root tip system ~ 15 mm Mantle 1000x

Morphology of Ectomycorrhizal System: dichotomous branched often straight system, light yellowish-brown tips, older tips darker, smooth reflective tips with pale root apex

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: none

Anatomy of Mantle in Plan View: thick net synenchyma, cells ~ 3m width, no visible septa or clamps, no visible cellular contents or ornamentation

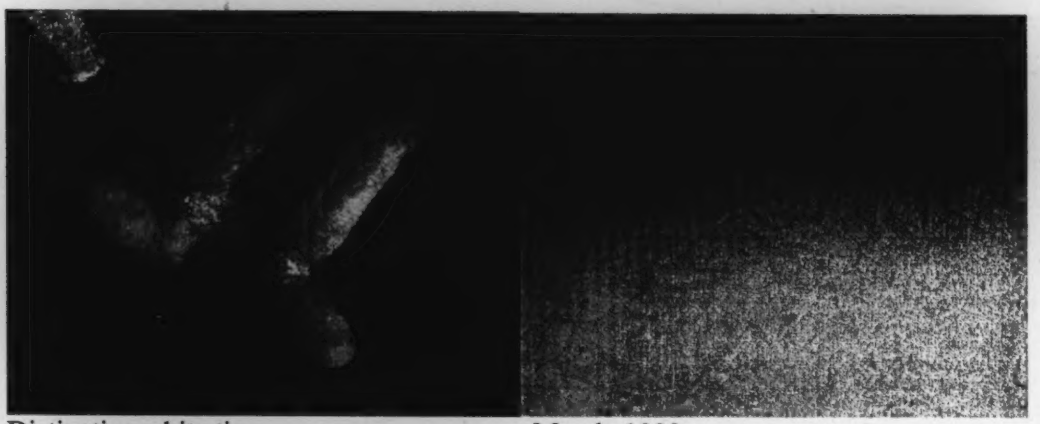
Other Features: cystidia absent

Morphological Type: *Laccaria* – like

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Agaricales
Family: Tricholomataceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: distinctive smooth creamy white tips



Distinctive white tips

Mantle 1000x

Morphology of Ectomycorrhizal System: non-branched or monopodial pinnate system, creamy white straight tips, older tips cottony and matte

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: frequent, cells 2-4 μm diameter, clear contents clamps common, H-shaped anastomoses present

Anatomy of Mantle in Plan View: loose net prosenchyma / synenchyma, cells clear no clamps or ornamentation, septa common

Other Features: cystidia absent, lacticifers absent

Morphological Type: MRA (*Mycelium radicis atrovirens*)

Phylum: Ascomycota
Class: Sordariomycetes
Order: Diaporthales
Family: Valsaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: dark brown to black root tips with felt like mantle

Root tip ~ 15mm Mantle 400x

Morphology of Ectomycorrhizal System: non-branched system, tips 3-5mm, brown to black, finely grainy, reflective, host visible through mantle

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: rare, straight

Anatomy of Mantle in Plan View: thin felt prosenchyma, dark brown cells ~ 2 μm diameter, no ornamentation or cellular contents, septa rare, no clamps

Other Features: cystidia absent

Morphological Type: *Piloderma* - like

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Stereales
Family: Atheliceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: ESSF mv2

Distinguishing Features: bright yellow emanating elements with loose felt prosenchyma mantle

Distinctive yellow hyphal fans Mantle 1000x

Morphology of Ectomycorrhizal System: distinctive bright yellow tips 3-10 mm length, straight non-branched, thick woolly hyphal fans, strands common, host completely obscured

Morphology of Mycelial Strands: common loose slightly differentiated, pronounced large ornamentation extremely verrucose, cells ~ 4 μm diameter clamps and anastomoses common

Morphology of Emanating Hyphae: very abundant curved to tortuous, pronounced large ornamentation extremely verrucose, cells ~ 4 μm diameter clamps and anastomoses common, difficult to determine if individual hyphae or part of mycelial strand

Anatomy of Mantle in Plan View: thick loose felt prosenchyma, cells ~ 4 µm wide, crystalline ornamentation and verrucose, septa and clamps common, H-shaped anastomoses common

Other Features: cystidia absent

Morphological Type: *Rhizopogon* – like I

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Boletales
Family: Rhizopogonaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: tuberculate system dark brown enclosing tan to white tips, emanating hyphae with distinctive elbow-like bends

Tuberculate root system

Mantle 1000x

Morphology of Ectomycorrhizal System: tuberculate root tip clusters, finely grainy dark brown outer surface, light brown to white tips, hyphae common light reddish-brown, no clamps with elbow like projections

Morphology of Mycelial Strands: rare, light brown to white, compact undifferentiated

Morphology of Emanating Hyphae: light reddish-brown, no clamps, clear no contents, distinctive elbow-like bends

Anatomy of Mantle in Plan View: thin linear net synenchyma, septa common no clamps, cells clear 1-2 μm wide

Other Features: cystidia absent

Morphological Type: *Rhizopogon* – like II

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Boletales
Family: Rhizopogonaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: monpodial pinnate system, tan to brown tips, abundant straight spiky emanating hyphae

Root tip system Mantle 1000x

Morphology of Ectomycorrhizal System: monopodial pinnate branching, tips slightly bent slightly tortuous, tips golden to pale brown, abundant linear hyphae reddish-brown

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: abundant straight spike-like, branched no clamps

Anatomy of Mantle in Plan View: thin linear net prosenchyma, long linear bands of cells, cells clear ~ 3 µm wide length varies, septa abundant no clamps

Other Features: cystidia absent

Morphological Type: *Suillus* – like I

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Boletales
Family: Suillaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: white to light brown tips with abundant hyphae and mycelial strands, tips in organized clumps

Root tip system

Hyphae, swollen septa, 1000x

Morphology of Ectomycorrhizal System: variable systems often hyphal fans, tips bent with dichotomous / coralloid / irregular branching, woolly with abundant hyphae and mycelial strands, tips smooth and finely grainy, pale brown to tan

Morphology of Mycelial Strands: loose or smooth, abundant, cells 3-5 μm wide, clear contents, no clamps septa swollen, distinctive verrucose crystalline ornamentation

Morphology of Emanating Hyphae: common, cells 3-5 μm wide, clear contents, no clamps septa swollen, distinctive verrucose crystalline ornamentation

Anatomy of Mantle in Plan View: mantle surface difficult to distinguish, thick loose felt prosenchyma, cells 3-5 μm wide, clear contents, no clamps septa swollen, distinctive verrucose crystalline ornamentation

Other Features: cystidia absent, H-shaped anastamoses common

Morphological Type: *Suillus* – like II

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Boletales
Family: Suillaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: tuberculate system, light brown to tan with abundant hyphae and mycelial strands

Tuberculate root system

Verrucose crystalline hyphae, 1000x

Morphology of Ectomycorrhizal System: tuberculate branching light brown to tan, thick mat of woolly hyphae abundant mycelial strands, hyphae with distinctive verrucose crystalline ornamentation, no clamps septa rare, tips smooth and finely grainy

Morphology of Mycelial Strands: common loose-undifferentiated, cells 3-5 μm wide, clear contents, no clamps septa rare, distinctive verrucose crystalline ornamentation

Morphology of Emanating Hyphae: abundant, cells 3-5 μm wide, clear contents, no clamps septa rare, distinctive verrucose crystalline ornamentation

Anatomy of Mantle in Plan View: mantle surface difficult to distinguish, thick loose felt prosenchyma, cells 3-5 μm wide, clear contents, no clamps septa rare, distinctive verrucose crystalline ornamentation

Other Features: cystidia absent

Morphological Type: *Thelephora* – like

Phylum: Basidiomycota
Class: Basidiomycotina
Order: Thelephorales
Family: Thelephoraceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2

Distinguishing Features: orange-brown tips with abundant basal clamped cystidia

Long branched orange-brown tips Mantle 1000x

Morphology of Ectomycorrhizal System: branched (monopodial pinnate or irregular) or not, tips various lengths, beige to orange-brown, smooth coarsely grainy and reflective

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: none

Anatomy of Mantle in Plan View: thin felt prosenchyma, cells 2-5 μm wide various lengths, clear no ornamentation, septa common no clamps

Other Features: awl shaped cystidia abundant with basal clamps, cells 1-4 µm wide and 50-300 μm long

Morphological Type: *Tomentella* – like I

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Thelephorales
Family: Thelephoraceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2

Distinguishing Features: tan to dark brown tips with distinctive regular synenchyma mantle

non-branched to irregular systems Mantle 1000x

Morphology of Ectomycorrhizal System: non-branched to irregular branching, tan to dark brown tips various sizes straight bent or tortuous, smooth to finely grainy, matte, host obscured

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: none

Anatomy of Mantle in Plan View: thick non-interlocking irregular synenchyma, clear cells ~ 4-8 μm diameter, septa and clamps common, no ornamentation

Other Features: cystidia absent

Morphological Type: *Tomentella* – like II

Phylum: Basidiomycota
Class: Homobasidiomycetes
Order: Thelephorales
Family: Thelephoraceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2

Distinguishing Features: non-branched single tip system, emanating hyphae and strands

Non-branched single tips Mantle 1000x

Morphology of Ectomycorrhizal System: non-branched straight or bent single tips, dark brown to black, coarsely grainy shiny reflective, obscures host

Morphology of Mycelial Strands: rare, wiry loose undifferentiated, finely verrucose

Morphology of Emanating Hyphae: common, finely verrucose no ornamentation, clamps no septa, cells 4-6 μm wide various lengths

Anatomy of Mantle in Plan View: thick non-interlocking irregular synenchyma and felt prosenchyma, clear cells ~ 5-7 μm diameter, septa and clamps common, no ornamentation

Other Features: awl shaped cystidia common, dark brown, cells ~ 10 μm basal, up to 100 μm length, clear no ornamentation, much shorter than hyphae

Morphological Type: *Tuber* – like

Phylum: Ascomycota
Class: Pezizomycetes
Order: Pezizales
Family: Tuberaceae

Host Species: *Pinus contorta* var. *latifolia*
Ecology: IDF dk2, ESSF mv2

Distinguishing Features: yellowish-brown tips with needle-like septate cystidia, cystidia may be confused with emanating hyphae

Tips straight to bent, various branching Mantle 1000x

Morphology of Ectomycorrhizal System: straight and bent yellowish-brown tips, dichotomous and monopodial pinnate branching, mostly smooth and reflective

Morphology of Mycelial Strands: none

Morphology of Emanating Hyphae: none

Anatomy of Mantle in Plan View: thin combination net prosenchyma and interlocking irregular synenchyma, cells clear no ornamentation ~ 5x10 μm septa common no clamps

Other Features: needle-like cystidia rare to common, thick walls ~ 3 μm wide various lengths